Final Author Comments for

Prediction of photosynthesis in Scots pine ecosystems across Europe by needle-level theory

by Pertti Hari et al. in Atmos. Chem. Phys. Discuss.

We are grateful to the reviewers for their insightful and detailed comments and have below replied (in red) to each of them individually.

Anonymous Referee #1

General comments:

1) The upscaling procedure deserves to be discussed in more detail. Because the leaf-level model is tested at the ecosystem scale, explaining the range of values of the ‘ecosystem-specific scaling coefficient’ is an essential part of assessing the role of ‘common regularities in the behavior of photosynthesis’ in ecosystem-atmosphere CO_2 exchange. In other words, when the modeled leaf-level flux is scaled to match measured ecosystem flux, does the scaling coefficient incorporate among-sites differences in canopy structure (leaf area and/or shoot structure) only? One could conjure a scenario in which, for example, both leaf area and photosynthetic efficiency change when moving from one stand to another. Why not compare estimates of GPP per unit leaf area across sites?

The most part of the “ecosystem –specific” behavior we describe in this paper is linked to temperature and introduced in the model via the S parameter. A minor part is dedicated to all other site-specific differences, LAI, moisture etc. The measure on a certain scale reflects the integrated or averaged value at that particular scale. Moving to larger scales is inevitably, accompanied by a loss in details. Moving from leaf level photosynthesis to EC data over a certain ecosystem’s footprint leads to loosing of detailed information on the variation within single leaves/branches, and we gain a more integrated/averaged value of the underlying fundamental process.

Thus, our scaling coefficient incorporates all these differences between sites, including e.g., differences in fine structure of needles, the functional properties of the photosynthetic machinery, canopy structure often described with LAI, site fertility and other factors. The variation of LAI ultimately scales also with a temperature gradient and LAI and photosynthetic efficiency are linearly linked to each other. So dividing GPP by unit leaf area will only change the slope if we express the result in logarithmic units.

Our theory opens numerous interesting possibilities to study photosynthesis such as analyzing the GPP per unit leaf area. However, these questions are outside of the focus of this study, since we are aiming to describe the applicability of the fundamental principles of the annual dynamics of photosynthesis in a large eco-climatic scale, and we believe adding more details would not be very useful for this analysis.

2) The structure of the paper would benefit from further streamlining. Related to the previous point, there is a range in the level of detail given, or depth of discussion, among various sections, which interferes with the flow of the paper. For example, the lack of consistent descriptions of the methods makes it difficult to follow (and to replicate) what was done. Also, it would be very helpful if all the parameters and drivers in all the equations were described and their units and fitted values (including the scaling coefficient) were given.

Response: We have rewritten parts of the paper and structured it to improve the clarity. The details of the model and especially the fundamental concept of the annual cycle has been published in Hari, P., et al. (2017) Annual cycle of Scots pine's photosynthesis, Atmos. Chem. Phys., 17, 15045-15053, https://doi.org/10.5194/acp-17-15045-2017), which is referred to in the text. A Table of parameters, units and fitted values was added (Table 1).

Specific comments:

P1L20-22: What do you mean by stable regularities? The study by Duursma et al. (2009, Tree Physiology 29, 621–639) appears relevant here.

Response: Thank you for pointing this out. With 'stable regularities' we mean here the fundamental and simple processes which can be scaled from smaller units to larger regions over the whole continent. Our approach is to develop here a model, which is robust enough to be applied for the annual variations of photosynthesis with very small number of environmental parameters and widely different climatic conditions.

We refer to the Duursma et al paper on p. 3 in the Introduction and on p. 6 in the discussion. Our results are in line with their analysis on conifer stand photosynthesis.

P3L15: Do you mean conifers from high latitudes?

Response: The annual cycle is a consequence of seasonal patterns in physical drivers of photosynthesis, most importantly temperature and irradiation. These changes cause a state change in the photosynthetic machinery from active to inactive state (e.g., transition from summer to winter) or vice versa. In some ecosystems the driver can be water availability which causes similar state changes. The text was revised to clarify that here we mean the trees in mid- and high latitudes experiencing seasonal temperature and irradiance changes.

P4L22: What do you mean by 'differences in species' here?

Response: This was a typo from previous version, we are grateful that the referee pointed it out. It was removed from the text.

P6L11-15: Please reduce repetition.

Response: Thanks for suggesting this, the text was rewritten and repetitions removed. We hope it now has a better structure and flow.

Fig.4: How do the residuals relate to soil moisture?

Response: The very small residuals in Figure 4 indicate that water stress or other environmental factors actually are of minor importance when the model incorporates the dynamic features of the annual dynamics of photosynthetic machinery.

Anonymous Referee #2

General comments:

1. I am not able to follow the modeling framework. A separate section for the model description is necessary. The model derivation in detail and a list of variables and units should be also provided in the Supplement. Is the adjustment in photosynthetic machinery due to the changes in temperature common for Scots pine? To my knowledge, the photosynthetic machinery in some species (e.g., Pinus edulis, Juniperus monosperma and Pinus taeda) even did not acclimate after long-term manipulation of precipitation and atmospheric CO2 concentration. The authors also pointed out that acclimation is omitted in the proposed model. However, how acclimation occurred at a longer time-scale is differentiated from the short-term changes in photosynthetic machinery needs further explanation.

Response: The model was presented in detail in Hari, P., et al. (2017) Annual cycle of Scots pine's photosynthesis, Atmos. Chem. Phys., 17, 15045-15053, https://doi.org/10.5194/acp-17-15045-2017), and therefore only the extension to the GPP annual dynamics is explained here. A Table of parameters, units and fitted values was added (Table 1).

It is evident that short-term acclimation and longer-term adaptation to environmental drivers need to be defined very carefully and have fundamentally very different consequences for plant physiology and thus also in any modeling exercise. Short-term changes in photosynthesis machinery are acclimations while longer timescale should be defined as adaptations. In terms of trees, the adaptation to high CO2 would need some reproduction cycles and changes on genomic level. Even the longest FACE experiments are still too short term to achieve this. On any scale in space and time, we should see adaptation of physiological processes as a “mean” and acclimation as some “noise” or “deviation” around that mean. Larger scales enable us to get higher accuracy information on the mean behavior, while smaller scales are better assessing the acclimation processes.

Long-term acclimation to precipitation or CO2 were not considered here, as we focused on the temperature and irradiation as short-term drivers of the annual dynamics state of photosynthetic machinery. However, in some ecosystems, periodic drought may have similar impact on the photosynthetic machinery as we observe here. Short-term acclimation to higher CO2 has an impact on the activity and quantity of the functional units involved, but the basic underlying processes are unlikely to change dramatically with increased CO2. Therefore, the model can be used for predicting the longer-term acclimation as well.

2. To predict GPP across the five Scots pine stands from leaf-level model, a scaling coefficient was used to bridge the two largely separated spatial scales. The scaling coefficient for current year was estimated by data from previous year. This suggests that the scaling coefficient is dynamic (i.e., yearly). What would be the information from this yearly scaling coefficient? When the dynamic of photosynthetic machinery is only estimated from one site and subsequently used for the other four sites, how would you interpret the differences in the scaling coefficients across the five sites?

Response: We assume that the scaling coefficient is not dynamic but rather stable within the site and characterizes the stand structure in an aggregated manner. We estimated the value from previous year to avoid estimation bias in the fit. We use the same parameter values for all sites. The differences in the parameter values is an additional source of variation in the value of the scaling factor.

3. I am not sure if the proposed model can accommodate the effects of water-stressed condition in the soil on stomatal conductance especially when the authors mainly focus on the responses to light and CO2. In fact, how the differences in the environmental factors impact the behavior of GPP across the five sites is not discussed in the manuscript. If water-stressed condition in the soil is not explicitly considered in the leaf-level model, do we expect that this information is embedded in the scaling coefficient?

Response: The setup of the model from theory incorporates the water stress in the optimal stomatal control. In that sense, using data to find parameters should yield in a set that has found the optimal stomatal control for a certain photosynthesis value in that case. Using a very large amount of data (large temporal scale even on leaf level) a "mean" optimal value should be found. This includes now also evidently local drought periods etc. This large temporal scale value is the one we use further on the ecosystem level.

Specific comments:

1. P2L22 Definition of stable regularities is needed.

Response: With 'stable regularities' we mean here the fundamental and simple processes which can be scaled from smaller units to larger regions over the whole continent. Our approach is to develop here a model, which is robust enough to be applied for the annual variations of photosynthesis with very small number of environmental parameters and widely different climatic conditions. ….

2. The order of Fig. 1 and 2 should be corrected to match the main text.

Response: Figures 1 and 2 have been changed in the text and their order of appearance as well.

3. Comparison between measured and modeled S (i.e., the state of photosynthetic machinery) as well as related discussions should be provided.

Response: The details in the model and especially the fundamental concept of the annual cycle has been published in Hari, et al. (2017) Annual cycle of Scots pine's photosynthesis, Atmos. Chem. Phys., 17, 15045-15053, https://doi.org/10.5194/acp-17-15045-2017),

4. P4L25 Description of up-scaling processes and the calculated scaling coefficient should be reported. Interpretation for the scaling coefficient is also required

Response: The scaling coefficient incorporates all differences between sites, such as differences in fine structure of leaves, differences in the photosynthetic machinery, (concentrations of pigments, membrane pumps and enzymes), differences in canopy structure often described with LAI, site fertility and others. See also the response to Ref 1, Q1.

5. P5L13-16 Is it possible that the photosynthetic parameters for the five sites are actually different but this information is embedded in scaling coefficient?

Response: We have described the scaling coefficient in our response to Ref 1, Q1. In brief, the GPP and also photosynthesis are scaling (and adapted) with temperature. The "mean" set of photosynthetic parameters will also scale with that. In northern ecosystems, less variability is observed in the "acclimation" to the specific stressors (drought, high light, etc.) and in southern ecosystems the deviations or "acclimations" are higher, generating more noise. That all can be said from the nature of the equation describing S.

6. P5L27-29 There are many models that can be used to predict stomatal conductance and then photosynthetic CO_2 flux in response to different environmental factors.

Response: Our purpose in this paper is to show that in order to predict the annual dynamics in photosynthesis, both stomatal conductance and the physiological processes related to the inherent carbon assimilation and light adsorbance, and - essentially - their synchronized assimilation to the system are needed. Our model includes the optimal stomatal control as the main factor for determining the CO2 diffusion to the site of photosynthesis. We have added more explanation on this aspect on p. 3 (lines 10-14).

7. Discussion regarding different environmental conditions (e.g., temperature, precipitation, soil water status…) across the five sites should be included. To do so, time series of environmental factors for the five sites should be also provided when comparing the measured with predicted GPP (i.e., fig 1 or 2?).

Response: The analysis of residuals (Fig 4) gives a good view of the range of conditions at each site during the measurements. It also shows the comparison between the GPP (modeled and predicted with the model). Therefore we did not add any new figure for this purpose. See also our responses to Scaling issues (Ref 1, Q1 and Ref 2, Q5)

Prediction of photosynthesis in Scots pine ecosystems across Europe by a needle-level theory

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Abstract. Photosynthesis provides carbon for the synthesis of macromolecules to construct cells during growth. This ~~fact ~~is the basis for~~generates~~ the key role of photosynthesis in the carbon dynamics of ecosystems ~~(Taiz et al., 2015) ~~and in the biogenic CO_2 ~~consumption~~assimilation. The development of eddy covariance measurements ~~of ~~for ecosystem CO_2 fluxes started a new era in the field studies of photosynthesis~~ (Baldocchi et al., 2000)~~. However, the interpretation of the very variable CO_2 fluxes in evergreen forests has been problematic especially in transition times such as the spring and autumn. We apply two theoretical needle-level equations that connect the variation in the light intensity, stomatal action and the annual metabolic cycle ~~with ~~of photosynthesis. We then ~~show that~~use these equations ~~are able ~~to predict ~~quite precisely and accurately ~~the photosynthetic CO_2 flux ~~between the atmosphere and different ecosystems ~~in five Scots pine stands located from northern timberline to Central Europe. Our result has strong implications on ~~the interpretation~~our conceptual understanding of the effects of the global change on the processes in boreal forests, especially of the changes in the metabolic annual cycle of photosynthesis.

1 Introduction

A large number of eddy-covariance (EC) measuring stations have been constructed into forests, peat lands, grasslands and agricultural fields (e.g., Baldocchi et al 2000). These stations have provided valuable insights into carbon and energy balances of various ecosystems, but the net fluxes measured with EC do not yield detailed information about the actual processes determining these fluxes. ~~The next~~Therefore, an important step forward ~~is to be able~~would be to ~~explain~~ connect the measured energy and carbon fluxes with the processes taking place in the vegetation and soil. In this way, one would obtain improved understanding of the changes in the metabolism and structure of ecosystems generated by the present global change~~, especially of the effects of increasing atmospheric CO_2 concentration and temperature~~.

~~. The measuring towers in Värriö (SMEAR I), Hyytiälä (SMEAR II), Norunda, Loobos and Brasschaat are located in Scots pine (*Pinus sylvestris*) stands (Fig. 1). We describe the measuring sites in more details in the Supplement.~~

The modeling of ~~eddy-covariance~~EC fluxes has received strong attention. The statistical approaches connect measured fluxes with environmental factors typically using rather simple 'big-leaf' models ~~whose~~ where parameters are determined from ecosystem-scale EC data (Land~~e~~sberg and Waring, 1997; Peltoniemi et al., 2015). More ~~theoretically~~ theory-driven modeling approaches are based on knowledge of plant metabolism, and account for the structure of the considered ecosystem. For instance, the widely used model by Farquhar et al. (1980) ~~developed a photosynthetic model~~is based on sound physiological knowledge on biochemical reactions, and it has been coupled with description of stomatal conductance to account for the effects of partial closure of stomata on leaf-scale photosynthesis and transpiration rate (Cowan and Farquhar, 1977; Collatz et al., 1991; Leuning, 1995; Mäkelä et al., 2004; Katul et al., 2010; Medlyn et al~~.,~~., 2011; Dewar et al., 2018). These coupled photosynthesis-stomatal conductance models are now widely adopted in vegetation and climate modelling (Chen et al., 1999; Krinner et al., 2005; Sitch et al., 2008; Lin et al., 2015), and also commonly evaluated against measured ~~eddy~~ EC fluxes (Wang et al., 2007). The upscaling from leaf to ecosystem scale is done either using 'big-leaf' approaches (dePury and Farquhar, 1997; Wang and Leuning, 1998), or by incorporating the impacts of vertical canopy structure on microclimatic drivers, solar radiation in particular, via multi-layer models of different complexity (Leuning, 1995; Baldocchi and Meyers, 1998).

~~However, these models have been unable to detect stable regularities at the European level.~~

~~It is well known that photosynthesis converts atmospheric CO_2 to organic intermediates and finally to sucrose in green foliage. This is done at sub-cellular scale by the actions of several, essential molecules: leaf pigment-protein complexes that capture the energy from light, simultaneously splitting water molecules; thylakoid membrane pumps and electron carriers that produce ATP (Adenosine Triphosphate) and NADPH (Nicotinamide adenine dinucleotide phosphate) with the captured energy, and finally enzymes in Calvin cycle that produce organic acids (phosphoglyceric acid) from atmospheric CO_2 utilizing ATP and NADPH (Calvin et al., 1950; Arnon et al., 1954a; Arnon et al., 1954b; Mitchell, 1961; Farquhar et al., 1980). The pigments, membrane pumps and enzymes form the photosynthetic machinery. The consumption of CO_2 in mesophyll chloroplasts~~

~~generates CO_2 flow from atmosphere into chloroplasts via stomata by diffusion (Farquhar and von Caemmerer, 1982; Harley et al., 1992), which widens the scale to the needle and shoot level.~~

The seasonal onset and decline of photosynthesis is closely following the temperature history, although in the short term and during the growing season photosynthesis follows primarily light (e.g. Kolari et al., 2007). Duursma et al. (2009) analysed the sensitivity in modeled stand photosynthesis (GPP) across six coniferous forests in Europe, using a photosynthesis model with submodels for light attenuation within the canopy and optimal stomatal control. They concluded that stand GPP was related to several aggregated weather variables, especially to the change in the effective temperature sum or mean annual temperature at the sites. They also concluded that quantum yield was the most influential parameter on annual GPP, followed by a parameter controlling the seasonality of photosynthesis and photosynthetic capacity. This is in line with our approach to include the light and temperature changes to the activity of the photosynthetic machinery in the model predicting stand-scale photosynthesis.

It is well known already for decades that photosynthesis converts atmospheric CO_2 to organic intermediates and finally to sucrose in green foliage, and involves both biochemical and physical processes. Biochemistry operates at sub-cellular scale by the actions of several essential molecules: pigment-protein complexes that capture the energy from light and simultaneously split water molecules; thylakoid membrane pumps and electron carriers that produce ATP (adenosine triphosphate) and NADPH (nicotinamide adenine dinucleotide phosphate) with the captured energy, and finally enzymes in the Calvin cycle that produce organic acids (phosphoglyceric acid) from atmospheric CO_2 utilizing the ATP and NADPH (Calvin et al., 1950; Arnon et al., 1954a; Arnon et al., 1954b; Mitchell, 1961; Farquhar et al., 1980). These pigments, membrane pumps and enzymes form the photosynthetic machinery required for the biochemistry. The physical part of photosynthesis involves the consumption of CO_2 in mesophyll chloroplasts, which generates CO_2 flow from atmosphere into chloroplasts via stomata by diffusion (Farquhar and von Caemmerer, 1982; Harley et al., 1992), and widens the scale of phenomena from molecular to the needle and shoot level. All C3 plants have a similar photosynthetic machinery that synthetizes sugars using light energy and atmospheric CO_2. This common functional basis generates common regularities in the behaviour of photosynthesis. The aim of our paper is to study the role of these regularities in the behaviour of the photosynthetic CO_2 flux, observed in the measurements at one site, Värriö, and use the above concepts to analyse the EC flux data in several Scots pine stands across Europe (Fig. 1).

2 Methods

Our purpose in this paper is to show that in order to predict the annual dynamics in photosynthesis of evergreen conifers, both stomatal conductance and the physiological processes related to the inherent carbon assimilation and light absorbance, and - essentially - their synchronized functioning in the system are needed. Therefore, w~~We~~ e involved both the biochemical and physical processes into the question of seasonality in evergreen canopy photosynthesis. In order to do this in a robust way, we followed the Newton's approach in discovering a way to construct equations to describe the diurnal behaviour of photosynthesis utilising knowledge of light and carbon reactions in photosynthesis (Hari et al., 2014, 2017). First, we defined concepts and introduced the fundamental features of light and carbon reactions of photosynthesis, the action of stomata, and diffusion of CO_2 (axioms). We finalised the theoretical analysis with the conservation of mass and evolutionary argument that combine the dominating features in the quantitative description of the system. In this way, we obtained an equation for the behaviour of photosynthesis of a leaf during a day $(p(I,E)_D)$ ~~Eq. (1). It~~that links the theoretical knowledge and climatic drivers (light, temperature, and CO_2 and water vapour concentration) to photosynthesis.

~~$p(I,E)=\frac{(u_{opt}\, g_{\max}\, C_a + r)\, b\, f(I)}{u_{opt}\, g_{\max} + b\, f(I)}$, (1)~~

$$p(I,E)_D = \frac{(u_{opt}\, g_{max}\, C_a + r)\, b\, f(I)}{u_{opt}\, g_{max} + b\, f(I)} \qquad (1)$$

Here, p is the rate of photosynthesis, E is transpiration rate, I is irradiation, ~~*where*~~ b is a parameter called the efficiency of photosynthesis, g_{max} is a parameter introducing stomatal conductance when stomata are fully open, r is the rate of respiration, and u_{opt} is optimal degree of stomatal opening obtained from as solution of the optimisation problem of stomatal behaviour (Hari et al 2014, 2017). The photosynthetic light response curve is given as $f(I)$ (see e.g., Mäkelä et al., 2004). Parameter values and units are given in Table 1.

We then analysed the annual cycle of evergreen foliage photosynthesis, by using~~.~~ as an example the common Eurasian evergreen tree species, Scots pine (*Pinus sylvestris* L.), as an example. Importantly, there is a strong annual cycle in the concentrations of active pigments, membrane pumps and enzymes, generating the distinctive ~~annual cycle~~seasonality in photosynthesis of evergreen foliage (Pelkonen and Hari, 1980; Öquist and Huner, 2003; Ensminger et al., 2004). The changing state of the photosynthetic machinery over the course of a year is a characteristic feature ~~of~~ determining the annual cycle of photosynthesis in coniferous trees, especially in mid and high latitudes experiencing seasonal temperature and irradiance changes. These state changes involve~~Scots pine has~~ a regulation system that synthetizes and decomposes pigments, membrane pumps and enzymes in the photosynthetic machinery. We introduced the fundamental behaviour of synthesis and decomposition to clarify the relationship between synthesis and temperature, and linked the synthesis and decomposition with the state of the photosynthetic machinery, S. Our mathematical analysis resulted in a simple differential equation (Hari et al., ~~submitted manuscript~~2017) that ~~describing~~ describes the behaviour of the state of thise photosynthetic machinery:~~. Eq. (2).~~

~~$\frac{dS}{dt} = Max\{0, a_1 (T - T_f)\} - a_2 S - a_3 Max\{(T_f - T) * I, 0\}$ (2)~~

$$\frac{dS}{dt} = Max\{0, a_1 \left(T + T_f\right)\} - a_2 S - a_3 Max\{\left(T_f - T\right) * I, 0\} \qquad (2)$$

Here, T_f is the freezing temperature of needles, T is the temperature, S is the state of photosynthetic machinery and a_1-a_3 are parameters describing the annual cycle of photosynthesis. We combined the state of photosynthetic machinery with the equation describing the photosynthesis during a day (Eq. (1)) to obtain a description of the annual GPP dynamics $p(I, E)_A$ (Eq 3). Our theoretical thinking determines the structure of these two equations.

~~$p(I, E) = \frac{(u_{opt}\, g_{\max}\, C_a + r)\, a_4\, S\, f(I)}{u_{opt}\, g_{\max} + a_4\, S\, f(I)}$ (3)~~

$$p(I, E)_A = \frac{\left(u_{opt}\, g_{max}\, C_a + r\right) a_4\, S\, f(I)}{u_{opt}\, g_{max} + a_4\, S\, f(I)} \qquad (3)$$

Here, g_{max} is the stomatal conductance at times when stomata are open, C_a is the CO$_2$ concentration in atmosphere, u_{opt} is the seasonal modulated degree of optimal stomatal control and a_4 is a parameter.

We estimated the values of the parameters in Eqs. (1) and (2) by analysing shoot-scale measurements of the CO$_2$ exchange ~~of~~ in evergreen Scots pine made during four years at our measuring station SMEAR I in Värriö, Northeastern Finland. To gain robust results, we used 130 000 measurements of photosynthetic CO$_2$ flux made with chambers. We found that Eqs. (1) and (2) together predicted photosynthesis very successfully, explaining about 95 % of the variance in the measured CO$_2$ flux at the shoot level ~~measured with chambers~~ (Hari et al., ~~submitted manuscript~~2017).

~~All Scots pines have the same photosynthetic machinery, i.e. pigments, membrane pumps and enzymes, that synthetize sugars using light energy and atmospheric CO$_2$. This common functional basis generates common regularities in the behaviour of photosynthesis. The aim of our paper is to study the role of the regularities, observed in the analysis of the chamber measurements in Värriö, in the behaviour of the photosynthetic CO$_2$ flux between Scots pine ecosystems and the atmosphere across Europe. . The measuring towers in Värriö (SMEAR I), Hyytiälä (SMEAR II), Norunda, Loobos and Brasschaat are located in Scots pine (*Pinus sylvestris*) stands (Fig. 1). We describe the measuring sites in more details in the Supplement.~~

~~2 Results~~

The ~~eddy-covariance~~EC methodology provides the mean CO_2 flux during some time interval, usually ~~0.5h~~30 min. In the case of a forest stand, t~~T~~he measured flux combines the photosynthesis of ~~pines~~ trees and of other vegetation growing on the site and, in addition, the respiration of plants and soil microbes. We extracted the ecosystem CO_2 flux generated by photosynthesis by removing respiration from the measurements with standard methods (Reichstein et al., 2005). In this way, we obtain the ~~CO_2 flux generated by photosynthesis in the~~ ecosystem-scale GPP time-series for all sites ~~and we call it gross primary production, GPP according to the common practice in the eddy-covariance research~~. We describe the measuring sites in more details in the Supplement.

We ~~want to~~ explored the role of regularities described with Eqs (1-3~~) and (2~~) in explaining variation of observed GPP in European pine forests.

Applying our equations dealing with the photosynthesis of one shoot to predict photosynthesis at ~~Scots pine~~ ecosystem level ~~in Europe~~ omits numerous additional phenomena apparent on that scale. These ~~omitted phenomena~~ include e.g. site-specific differences in the structure of shoots and canopy, adaption and acclimation of structure and metabolism to e.g. water availability, ~~difference in species,~~ and ~~in~~ extinction of light in the canopy, etc. ~~We expect that t~~These omitted phenomena generate noise in the prediction of photosynthesis at ecosystem level and consequently reduce goodness of fit of the prediction of GPP. ~~We want to explore the role of regularities described with Eqs (1) and (2) in explaining variation of observed GPP in European pine forests.~~

Therefore, the transition from ~~the~~ leaf ~~level~~ to ~~the~~ ecosystem level ~~when utilising our equations~~ requires a rough description of the differences between shoot and ecosystem, and between ecosystems. We describe these differences with an ~~ecosystem~~ ecosystem-specific scaling coefficient. As the first step of the prediction, we determined the values of the scaling coefficients from measurements done at each site during the year ~~previous to~~preceding the one we ~~wanted~~ were aiming to predict. Thereafter we were able to predict the GPP in the five ~~ecosystems~~ pine stands in Europe. We based our prediction utilising the two equations on the measured values of light, temperature and CO_2 and water vapour concentrations done in each site, on the parameter value obtained ~~in~~by the ~~chamber~~ shoot-scale measurements in Värriö, and on the site-specific scaling coefficients determined from the eddy-covariance measurements done on the sites during the previous year. We developed a code in MatLab to perform the predictions.

3 Results

The predictions obtained for all measured Scots pine ecosystems were successful ~~(Fig. 2)~~ in describing the dynamic features of GPP (Fig. 2).

The ~~predictions of the~~ daily patterns of ~~measured~~ modeled photosynthetic CO_2 fluxes are very similar to the measured ones in each studied ecosystem throughout the photosynthetically active period. The predictions capture adequately the daily patterns: rapid increase of GPP after sunrise, its saturation in the middle of the day, and its decline when the light intensity is decreasing towards evening. Clear proofs of its predictive power on a daily scale are the occasions when c~~C~~louds reduce the light intensity to variable degrees, causing rapid variations in the CO_2 flux (Fig 2, Brasschaat day 186 and 187) and strong reduction in the CO_2 flux ~~in this flux~~ on days with heavy clouds (Fig 2, day 184 in Värriö and day 213 in Norunda).

The patterns found in the annual cycle of photosynthesis are very different at the different measurement sites in Europe. We defined the onset of photosynthesis at each site as the moment when the running mean of 14 days of photosynthetic CO_2 flux exceeds 20 % of the corresponding running mean in midsummer, and the moment of cessation of photosynthesis as the moment when the running mean of ~~CO_2 flux~~GPP has declined to 20 % of its summer time value. Our prediction of the timing of onset and cessation ~~moments~~ of photosynthesis in the different measuring sites was quite successful, and~~s~~ the observed and predicted dates ~~of the onset and cessation of photosynthesis~~ were very close to each other at ~~different~~ all measurement sites (Fig. 3 panels A and B). Surprisingly, the parameter values in the differential equation dealing with the annual dynamics. i.e., the synthesis and decomposition of the photosynthetic machinery, obtained from ~~chamber~~ shoot-scale measurements in Värriö, seemed to produce quite adequate predictions at ecosystem level in the other studied Scots pine stands although they are growing in very different climates.

The prediction power of GPP by our equations in five Scots pine ecosystems in Scandinavia and in Central Europe was higher than what we expected. The equations predicted successfully the rapid variations in all studied ecosystems, even though the residual variation was evidently a bit larger in the southern than in the northern ecosystems (Fig. 4). Our predictions using the parameters from Värriö explained about 80 % of the variance of photosynthetic CO_2 flux in the measured ecosystems. The maximum proportion of explained variance was 93 % in SMEAR II and minimum 75 % in Brasschaat. Due to t~~T~~he quite large measuring noise of eddy-covariance measurements, ~~is quite large,~~ about 10–30 % (Rannik et al., 2004; Richardson et al., 2006), it probably ~~therefore~~ dominates the residuals, i.e. the difference between measured and predicted fluxes. We ~~further~~ studied further the residuals as function of light, temperature, CO_2 and water vapour concentration (Fig. 4), but~~. We~~ detected only minor systematic behaviour in the residuals, indicating that these factors were not determining the difference between the measured and predicted values. To analyse the robustness of the results when scaled from leaf to stand scale, we also tested the difference between sites in the modelled and measured GPP when the ecosystem-specific scaling coefficient was based on the reported leaf area indexes, and these results (analysis not shown) indicate that the dynamics of ecosystem-level photosynthesis are rather independent of LAI values. This shows that the functional regularities determined in the model structure are able to capture the essential processes in the evergreen foliage photosynthesis.

~~The prediction power of GPP by our equations in five Scots pine ecosystems in Scandinavia and in Central Europe was higher than what we expected. The equations predicted successfully the rapid variation in all studied ecosystems, even though the residual variation was evidently a bit larger in the southern than in the northern ecosystems (Fig. 4).~~

~~3~~4 Discussion and conclusions

Although the annual behaviour of carbon exchange in ecosystems is rather well documented as a phenomenon, we have found no theory/model that links the variations in environmental factors and the photosynthetic CO_2 flux of Scots pine ecosystems during a yearly cycle. Our results are in line with Duursma et al (2009) who tested the relative importance of climate, canopy structure and leaf physiology across a gradient of forest stands in Europe, and concluded that the annual dynamics of photosynthesis was closely connected to seasonal temperature variations and the temperature sums. However, their model explained only 62% of variation in annual GPP across site-years, due to their model structure which was more sensitive to soil moisture or leaf area changes. ~~Consequently, we are unable to compare our results with results reported in the literature.~~

Our result that the behaviour of measured gross primary production in Scots pine stands follows the same equations in a large area in Europe from the northern timber line to the strongly polluted areas in Central Europe near the southern edge of the Scots pine growing area opens new possibilities for investigating ~~research of~~ carbon budgets of ~~Scots pine~~evergreen forest ecosystems. The light and carbon reactions and the stomatal actions determine the daily behaviour of CO_2 flux between the Scots pine ecosystem and the atmosphere. Temperature has a dominating role in the dynamics of the annual cycle of photosynthesis.

The present global climate change stresses the importance to understand the ecosystem responses to increasing atmospheric CO_2 concentration and temperature. ~~The~~ E~~e~~quations 1 and 2 resulted in an adequate prediction of the GPP for all five studied Scots pine ecosystems. We can expect that the differential equation provides also adequate predictions of the photosynthetic response to a temperature increase in Lapland when th~~is temperature~~e increase is smaller than the mean temperature difference between Värriö and Brasschaat, i.e. about 10 °C. ~~The e~~Equations 1 and 2 provide also a prediction of the photosynthetic response of Scots pine ecosystems to increasing atmospheric CO_2 concentration, ~~. This response is~~ based on changes in carbon reactions of photosynthesis. The physiological basis of the photosynthetic response in the model is sound and, in addition, the residuals of our prediction show no clear trend as function of atmospheric CO_2 concentration (Fig. 4).

The prediction of daily and annual behaviour of photosynthesis based on the presented two equations was successful in five Scots pine ecosystems, expanding from northern timberline to Central Europe. T~~hus, t~~he regularities observed in the ~~chamber~~ shoot-scale measurements in Värriö seem to play a very important role in the photosynthetic CO_2 flux ~~between Scots pine~~in evergreen Scots pine ecosystems ~~and the atmosphere in five stands from arctic Lapland to Central Europe~~across quite large geographical range. ~~The obtained result indicates that there are common regularities in the photosynthesis of Scots pine over Europe.~~ Our result provides some justification to think that there are also other common regularities in the behaviour of forests to be discovered.

Data availability

Data measured at the SMEAR I and II stations is available on the following website: http://avaa.tdata.fi/web/smart/. The data is licensed under a Creative Commons 4.0 Attribution (CC BY) license. Data measured at Norunda, Brasschaat and Loobos is available via ICOS Carbon Portal. Model codes can be obtained from Pertti Hari upon request (pertti.hari@helsinki.fi).

Competing interests

The authors declare that they have no conflict of interest.

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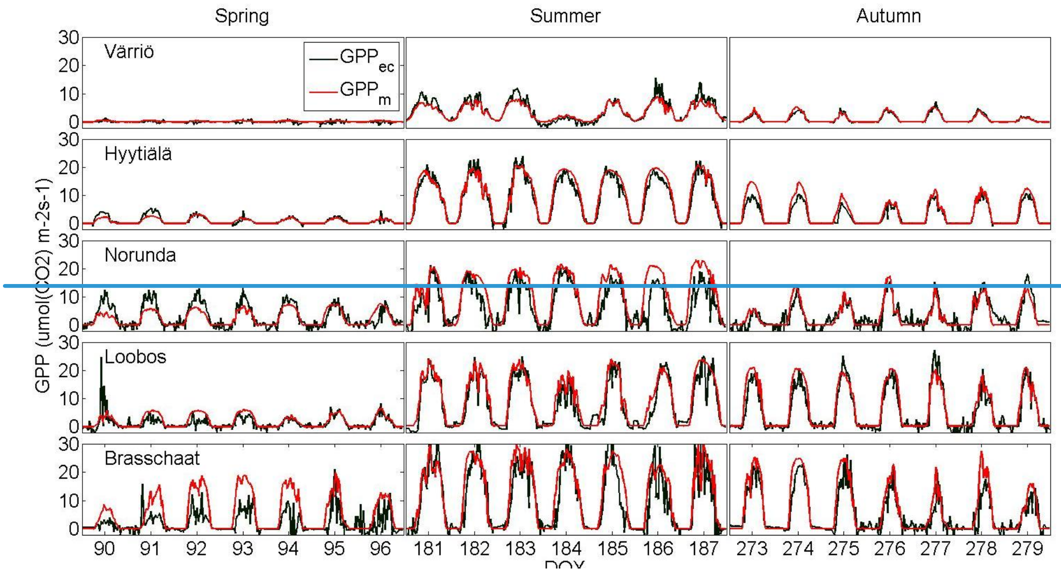
Table 1. Symbols and parameters in model equations

Name of parameter	**S~~s~~ymbol**	**U~~u~~nit**	**N~~n~~otes**
Rate of photosynthesis	p	µmol CO_2 m^{-2} s^{-1}	
Rate of transpiration	E	mmol H_2O m^{-2} s^{-1}	
Photosynthetically active irradiation	I	µmol photons m^{-2} s^{-1}	
Efficiency of photosynthesis	b	µmol g m^{-5} s^{-1}	
Stomatal conductance when stomata are fully open	g_{max}	mmol H_2O m^{-2} s^{-1}	
Optimal degree of stomatal opening	u_{opt}	unitless	
CO_2 concentration in ambient air	C_a	g m^{-3}	
Rate of respiration	r	µmol CO_2 m^{-2} s^{-1}	
Temperature	T	K	
State of photosynthetic machinery	S	unitless	
Parameters describing the annual cycle of photosynthesis, estimated using numeric methods (see Hari et al 2017)	a1 … a4		a1 = 10 a2 = 0.065 a3 = 2 a4 = $1.15 * 10^{-7}$



~~**Figure 1. The measured (black) and predicted (purple) photosynthetic CO$_2$ flux (GPP) between forest ecosystem and the atmosphere as function of time in five eddy-covariance measuring sites in Europe during a week in early spring, summer and autumn.**~~

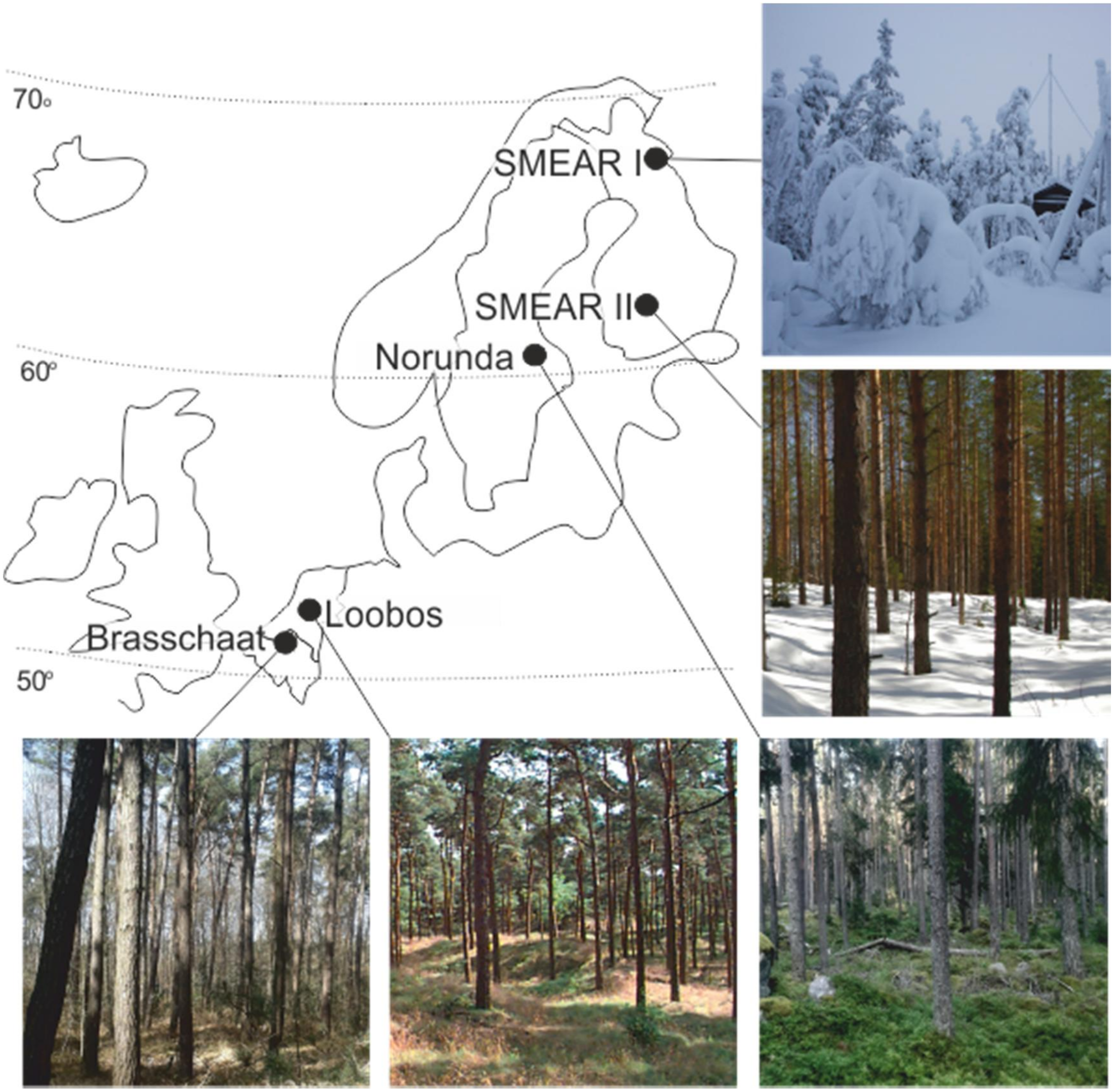


Figure ~~2~~1. The location of the measuring stations in Europe and photos of the stands. The photo of SMEAR I is taken around Christmas time, SMEAR II early spring, Norunda, Loobos and Brasschaat in summer time.

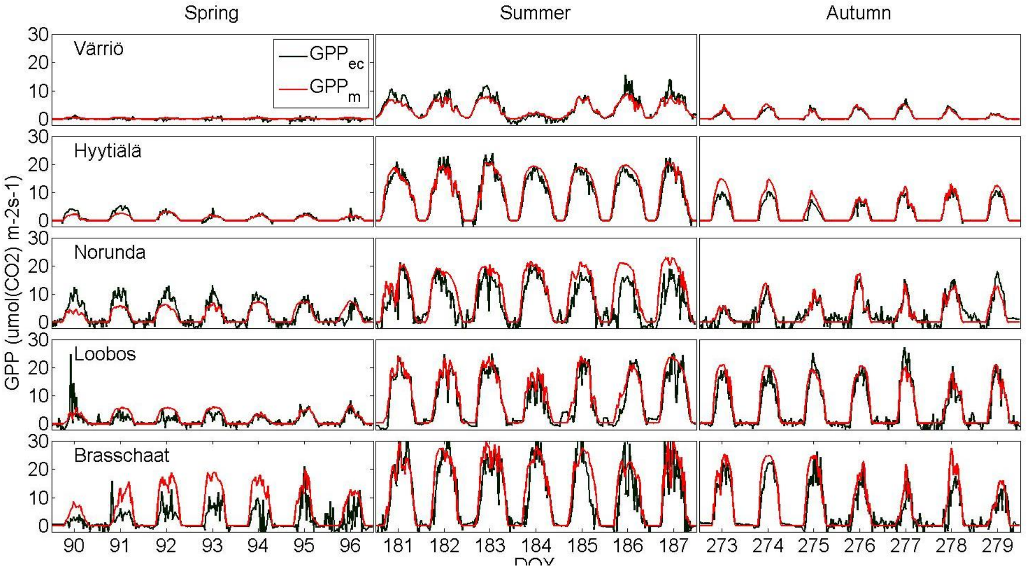


Figure 2. The measured (black) and predicted (purple) photosynthetic CO_2 flux (GPP) between forest ecosystem and the atmosphere as function of time in five eddy-covariance measuring sites in Europe during a week in early spring, summer and autumn.

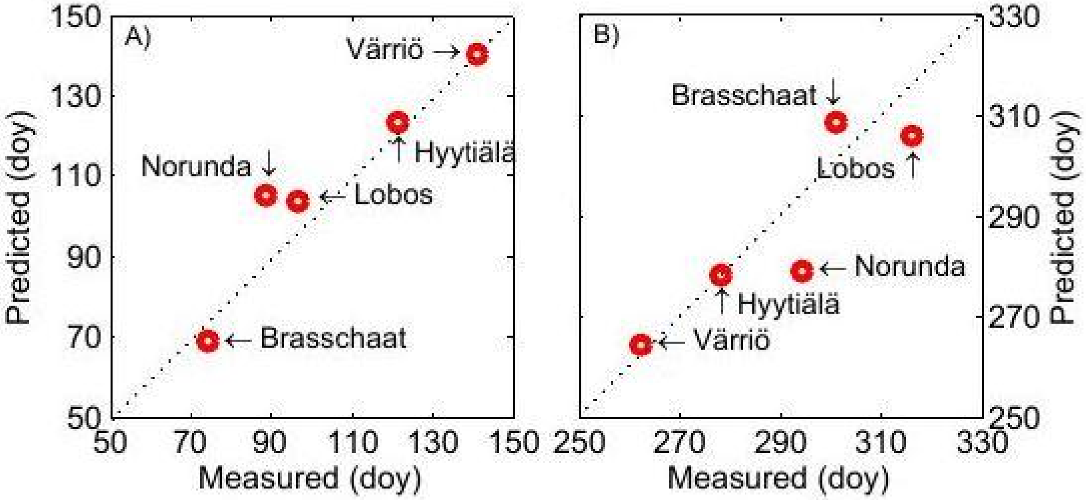


Figure 3. A The relationship between measured and predicted onset and cessation dates of photosynthesis in the five studied ecosystems, B the cessation dates of photosynthesis in the five ecosystems.

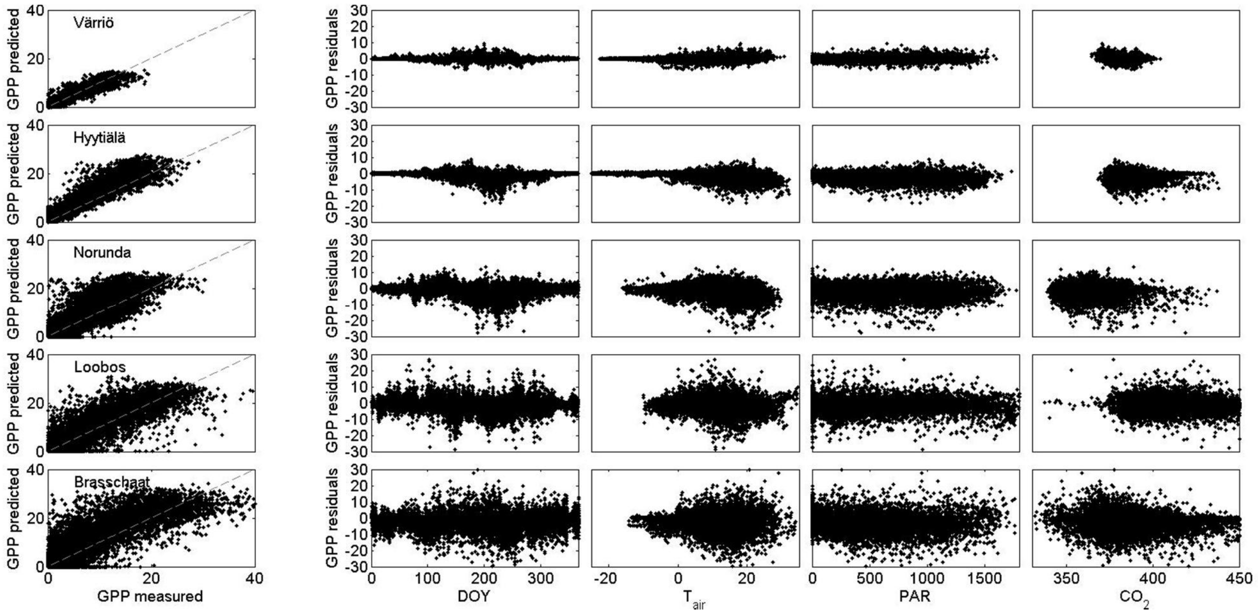


Figure 4. The relationship between measured and predicted gross primary production (the first column). Columns 2-4 present the residuals as function of time, air temperature, photosynthetically active radiation and carbon dioxide concentration.

Prediction of photosynthesis in Scots pine ecosystems across Europe by a needle-level theory

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Abstract. Photosynthesis provides carbon for the synthesis of macromolecules to construct cells during growth. This is the basis for the key role of photosynthesis in the carbon dynamics of ecosystems and in the biogenic CO_2 assimilation. The development of eddy covariance measurements for ecosystem CO_2 fluxes started a new era in the field studies of photosynthesis. However, the interpretation of the very variable CO_2 fluxes in evergreen forests has been problematic especially in transition times such as the spring and autumn. We apply two theoretical needle-level equations that connect the variation in the light intensity, stomatal action and the annual metabolic cycle of photosynthesis. We then use these equations to predict the photosynthetic CO_2 flux in five Scots pine stands located from northern timberline to Central Europe. Our result has strong implications on our conceptual understanding of the effects of the global change on the processes in boreal forests, especially of the changes in the metabolic annual cycle of photosynthesis.

1 Introduction

A large number of eddy-covariance (EC) measuring stations have been constructed into forests, peat lands, grasslands and agricultural fields (e.g., Baldocchi et al 2000). These stations have provided valuable insights into carbon and energy balances of various ecosystems, but the net fluxes measured with EC do not yield detailed information about the actual processes determining these fluxes. Therefore, an important step forward would be to connect the measured energy and carbon fluxes with the processes taking place in the vegetation and soil. In this way, one would obtain improved understanding of the changes in the metabolism and structure of ecosystems generated by the present global change.

The modeling of EC fluxes has received strong attention. The statistical approaches connect measured fluxes with environmental factors typically using rather simple ‘big-leaf’ models where parameters are determined from ecosystem-scale EC data (Landsberg and Waring, 1997; Peltoniemi et al., 2015). More theory-driven modeling approaches are based on knowledge of plant metabolism, and account for the structure of the considered ecosystem. For instance, the widely used model by Farquhar et al. (1980) is based on sound physiological knowledge on biochemical reactions, and it has been coupled with description of stomatal conductance to account for the effects of partial closure of stomata on leaf-scale photosynthesis and transpiration rate (Cowan and Farquhar, 1977; Collatz et al., 1991; Leuning, 1995; Mäkelä et al., 2004; Katul et al., 2010; Medlyn et al., 2011; Dewar et al., 2018). These coupled photosynthesis-stomatal conductance models are now widely adopted in vegetation and climate modelling (Chen et al., 1999; Krinner et al., 2005; Sitch et al., 2008; Lin et al., 2015), and also commonly evaluated against measured EC fluxes (Wang et al., 2007). The upscaling from leaf to ecosystem scale is done either using ‘big-leaf’ approaches (dePury and Farquhar, 1997; Wang and Leuning, 1998), or by incorporating the impacts of vertical canopy structure on microclimatic drivers, solar radiation in particular, via multi-layer models of different complexity (Leuning, 1995; Baldocchi and Meyers, 1998).

The seasonal onset and decline of photosynthesis is closely following the temperature history, although in the short term and during the growing season photosynthesis follows primarily light (e.g. Kolari et al., 2007). Duursma et al. (2009) analysed the sensitivity in modeled stand photosynthesis (GPP) across six coniferous forests in Europe, using a photosynthesis model with submodels for light attenuation within the canopy and optimal stomatal control. They concluded that stand GPP was related to several aggregated weather variables, especially to the change in the effective temperature sum or mean annual temperature at the sites. They also concluded that quantum yield was the most influential parameter on annual GPP, followed by a parameter controlling the seasonality of photosynthesis and photosynthetic capacity. This is in line with our approach to include the light and temperature changes to the activity of the photosynthetic machinery in the model predicting stand-scale photosynthesis.

It is well known already for decades that photosynthesis converts atmospheric CO_2 to organic intermediates and finally to sucrose in green foliage, and involves both biochemical and physical processes. Biochemistry operates at sub-cellular scale by the actions of several essential molecules: pigment-protein complexes that capture the energy from light and simultaneously split water molecules; thylakoid membrane pumps and electron carriers that produce ATP (adenosine triphosphate) and NADPH (nicotinamide adenine dinucleotide phosphate) with the captured energy, and finally enzymes in the Calvin cycle that produce organic acids (phosphoglyceric acid) from atmospheric CO_2 utilizing the ATP and NADPH (Calvin et al., 1950; Arnon et al., 1954a; Arnon et al., 1954b; Mitchell, 1961; Farquhar et al., 1980). These pigments, membrane pumps and enzymes form the photosynthetic machinery required for the biochemistry. The physical part of photosynthesis involves the consumption of CO_2 in mesophyll chloroplasts, which generates CO_2 flow from atmosphere into chloroplasts via stomata by diffusion (Farquhar and von Caemmerer, 1982; Harley et al., 1992), and widens the scale of phenomena from molecular to the needle and shoot level. All C3 plants have a similar photosynthetic machinery that synthetizes sugars using light energy and atmospheric CO_2. This common functional basis generates common regularities in the behaviour of photosynthesis. The aim of our paper is to study the role of these regularities in the behaviour of the photosynthetic CO_2 flux, observed in the measurements at one site, Värriö, and use the above concepts to analyse the EC flux data in several Scots pine stands across Europe (Fig. 1).

2 Methods

Our purpose in this paper is to show that in order to predict the annual dynamics in photosynthesis of evergreen conifers, both stomatal conductance and the physiological processes related to the inherent carbon assimilation and light absorbance, and - essentially - their synchronized functioning in the system are needed. Therefore, we involved both the biochemical and physical processes into the question of seasonality in evergreen canopy photosynthesis. In order to do this in a robust way, we followed the Newton's approach in discovering a way to construct equations to describe the diurnal behaviour of photosynthesis utilising knowledge of light and carbon reactions in photosynthesis (Hari et al., 2014, 2017). First, we defined concepts and introduced the fundamental features of light and carbon reactions of photosynthesis, the action of stomata, and diffusion of CO_2 (axioms). We finalised the theoretical analysis with the conservation of mass and evolutionary argument that combine the dominating features in the quantitative description of the system. In this way, we obtained an equation for the behaviour of photosynthesis of a leaf during a day ($p(I, E)_D$) that links the theoretical knowledge and climatic drivers (light, temperature, and CO_2 and water vapour concentration) to photosynthesis.

$$p(I, E)_D = \frac{\left(u_{opt}\, g_{max}\, C_a + r\right)\, b\, f(I)}{u_{opt}\, g_{max} + b\, f(I)} \qquad (1)$$

Here, p is the rate of photosynthesis, E is transpiration rate, I is irradiation, b is a parameter called the efficiency of photosynthesis, g_{max} is a parameter introducing stomatal conductance when stomata are fully open, r is the rate of respiration, and u_{opt} is optimal degree of stomatal opening obtained from as solution of the optimisation problem of stomatal behaviour (Hari et al 2014, 2017). The photosynthetic light response curve is given as $f(I)$ (see e.g., Mäkelä et al., 2004). Parameter values and units are given in Table 1.

We then analysed the annual cycle of evergreen foliage photosynthesis, by using as an example the common Eurasian evergreen tree species, Scots pine (*Pinus sylvestris* L.), as an example. Importantly, there is a strong annual cycle in the concentrations of active pigments, membrane pumps and enzymes, generating the distinctive seasonality in photosynthesis of evergreen foliage (Pelkonen and Hari, 1980; Öquist and Huner, 2003; Ensminger et al., 2004). The changing state of the photosynthetic machinery over the course of a year is a characteristic feature determining the annual cycle of photosynthesis in coniferous trees, especially in mid and high latitudes experiencing seasonal temperature and irradiance changes. These state changes involve a regulation system that synthetizes and decomposes pigments, membrane pumps and enzymes in the photosynthetic machinery. We introduced the fundamental behaviour of synthesis and decomposition to clarify the relationship between synthesis and temperature, and linked the synthesis and decomposition with the state of the photosynthetic machinery, S. Our mathematical analysis resulted in a simple differential equation (Hari et al., 2017) that describes the behaviour of the state of this photosynthetic machinery:

$$\frac{dS}{dt} = Max\{0, a_1\left(T + T_f\right)\} - a_2S - a_3Max\{\left(T_f - T\right) * I, 0\} \qquad (2)$$

Here, T_f is the freezing temperature of needles, T is the temperature, S is the state of photosynthetic machinery and a_1-a_3 are parameters describing the annual cycle of photosynthesis. We combined the state of photosynthetic machinery with the equation describing the photosynthesis during a day (Eq. (1)) to obtain a description of the annual GPP dynamics $p(I, E)_A$ (Eq 3). Our theoretical thinking determines the structure of these two equations.

$$p(I, E)_A = \frac{\left(u_{opt}\, g_{max}\, C_a + r\right) a_4\, S\, f(I)}{u_{opt}\, g_{max} + a_4\, S\, f(I)} \qquad (3)$$

Here, g_{max} is the stomatal conductance at times when stomata are open, C_a is the CO_2 concentration in atmosphere, u_{opt} is the seasonal modulated degree of optimal stomatal control and a_4 is a parameter.

We estimated the values of the parameters in Eqs. (1) and (2) by analysing shoot-scale measurements of the CO_2 exchange in evergreen Scots pine made during four years at our measuring station SMEAR I in Värriö, Northeastern Finland. To gain robust results, we used 130 000 measurements of photosynthetic CO_2 flux made with chambers. We found that Eqs. (1) and (2) together predicted photosynthesis very successfully, explaining about 95 % of the variance in the measured CO_2 flux at the shoot level (Hari et al., 2017).

The EC methodology provides the mean CO_2 flux during some time interval, usually 30 min. In the case of a forest stand, the measured flux combines the photosynthesis of trees and of other vegetation growing on the site and, in addition, the respiration of plants and soil microbes. We extracted the ecosystem CO_2 flux generated by photosynthesis by removing respiration from the measurements with standard methods (Reichstein et al., 2005). In this way, we obtain the ecosystem-scale GPP time-series for all sites. We describe the measuring sites in more details in the Supplement.

We explored the role of regularities described with Eqs (1-3) in explaining variation of observed GPP in European pine forests. Applying our equations dealing with the photosynthesis of one shoot to predict photosynthesis at ecosystem level omits numerous additional phenomena apparent on that scale. These include e.g. site-specific differences in the structure of shoots and canopy, adaption and acclimation of structure and metabolism to e.g. water availability, and extinction of light in the canopy, etc. These omitted phenomena generate noise in the prediction of photosynthesis at ecosystem level and consequently reduce goodness of fit of the prediction of GPP. Therefore, the transition from leaf to ecosystem level requires a rough description of the differences between shoot and ecosystem, and between ecosystems. We describe these differences with an ecosystem-specific scaling coefficient. As the first step of the prediction, we determined the values of the scaling coefficients from measurements done at each site during the year preceding the one we were aiming to predict. Thereafter we were able to predict the GPP in the five pine stands in Europe. We based our prediction utilising the two equations on the measured values of light, temperature and CO_2 and water vapour concentrations done in each site, on the parameter value obtained by the shoot-scale measurements in Värriö, and on the site-specific scaling coefficients determined from the eddy-covariance measurements done on the sites during the previous year. We developed a code in MatLab to perform the predictions.

3 Results

The predictions obtained for all measured Scots pine ecosystems were successful in describing the dynamic features of GPP (Fig. 2). The daily patterns of modeled photosynthetic CO_2 fluxes are very similar to the measured ones in each studied ecosystem throughout the photosynthetically active period. The predictions capture adequately the daily patterns: rapid increase of GPP after sunrise, its saturation in the middle of the day, and its decline when the light intensity is decreasing towards evening. Clear proofs of its predictive power on a daily scale are the occasions when clouds reduce the light intensity to variable degrees, causing rapid variations in the CO_2 flux (Fig 2, Brasschaat day 186 and 187) and strong reduction in the CO_2 flux on days with heavy clouds (Fig 2, day 184 in Värriö and day 213 in Norunda).

The patterns found in the annual cycle of photosynthesis are very different at the different measurement sites in Europe. We defined the onset of photosynthesis at each site as the moment when the running mean of 14 days of photosynthetic CO_2 flux exceeds 20 % of the corresponding running mean in midsummer, and the moment of cessation of photosynthesis as the moment when the running mean of GPP has declined to 20 % of its summer time value. Our prediction of the timing of onset and cessation of photosynthesis in the different measuring sites was quite successful, and the observed and predicted dates were very close to each other at all measurement sites (Fig. 3 panels A and B). Surprisingly, the parameter values in the differential equation dealing with the annual dynamics. i.e., the synthesis and decomposition of the photosynthetic machinery, obtained from shoot-scale measurements in Värriö, seemed to produce quite adequate predictions at ecosystem level in the other studied Scots pine stands although they are growing in very different climates.

The prediction power of GPP by our equations in five Scots pine ecosystems in Scandinavia and in Central Europe was higher than what we expected. The equations predicted successfully the rapid variations in all studied ecosystems, even though the residual variation was evidently a bit larger in the southern than in the northern ecosystems (Fig. 4). Our predictions using the parameters from Värriö explained about 80 % of the variance of photosynthetic CO_2 flux in the measured ecosystems. The maximum proportion of explained variance was 93 % in SMEAR II and minimum 75 % in Brasschaat. Due to the quite large measuring noise of eddy-covariance measurements, about 10–30 % (Rannik et al., 2004; Richardson et al., 2006), it probably dominates the residuals, i.e. the difference between measured and predicted fluxes. We studied further the residuals as function of light, temperature, CO_2 and water vapour concentration (Fig. 4), but detected only minor systematic behaviour in the residuals, indicating that these factors were not determining the difference between the measured and predicted values. To analyse the robustness of the results when scaled from leaf to stand scale, we also tested the difference between sites in the modelled and measured GPP when the ecosystem-specific scaling coefficient was based on the reported leaf area indexes, and these results (analysis not shown) indicate that the dynamics of ecosystem-level photosynthesis are rather independent of LAI values. This shows that the functional regularities determined in the model structure are able to capture the essential processes in the evergreen foliage photosynthesis.

4 Discussion and conclusions

Although the annual behaviour of carbon exchange in ecosystems is rather well documented as a phenomenon, we have found no theory/model that links the variations in environmental factors and the photosynthetic CO_2 flux of Scots pine ecosystems during a yearly cycle. Our results are in line with Duursma et al (2009) who tested the relative importance of climate, canopy structure and leaf physiology across a gradient of forest stands in Europe, and concluded that the annual dynamics of photosynthesis was closely connected to seasonal temperature variations and the temperature sums. However, their model explained only 62% of variation in annual GPP across site-years, due to their model structure which was more sensitive to soil moisture or leaf area changes.

Our result that the behaviour of measured gross primary production in Scots pine stands follows the same equations in a large area in Europe from the northern timber line to the strongly polluted areas in Central Europe near the southern edge of the Scots pine growing area opens new possibilities for investigating carbon budgets of evergreen forest ecosystems. The light and carbon reactions and the stomatal actions determine the daily behaviour of CO_2 flux between the Scots pine ecosystem and the atmosphere. Temperature has a dominating role in the dynamics of the annual cycle of photosynthesis.

The present global climate change stresses the importance to understand the ecosystem responses to increasing atmospheric CO_2 concentration and temperature. Equations 1 and 2 resulted in an adequate prediction of the GPP for all five studied Scots pine ecosystems. We can expect that the differential equation provides also adequate predictions of the photosynthetic response to a temperature increase in Lapland when the increase is smaller than the mean temperature difference between Värriö and Brasschaat, i.e. about 10 °C. Equations 1 and 2 provide also a prediction of the photosynthetic response of Scots pine ecosystems to increasing atmospheric CO_2 concentration, based on changes in carbon reactions of photosynthesis. The physiological basis of the photosynthetic response in the model is sound and, in addition, the residuals of our prediction show no clear trend as function of atmospheric CO_2 concentration (Fig. 4).

The prediction of daily and annual behaviour of photosynthesis based on the presented two equations was successful in five Scots pine ecosystems, expanding from northern timberline to Central Europe. The regularities observed in the shoot-scale measurements in Värriö seem to play a very important role in the photosynthetic CO_2 flux in evergreen Scots pine ecosystems across quite large geographical range. Our result provides some justification to think that there are also other common regularities in the behaviour of forests to be discovered.

Data availability

Data measured at the SMEAR I and II stations is available on the following website: http://avaa.tdata.fi/web/smart/. The data is licensed under a Creative Commons 4.0 Attribution (CC BY) license. Data measured at Norunda, Brasschaat and Loobos is available via ICOS Carbon Portal. Model codes can be obtained from Pertti Hari upon request (pertti.hari@helsinki.fi).

Competing interests

The authors declare that they have no conflict of interest.

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Table 1. Symbols and parameters in model equations

Name of parameter	**Symbol**	**Unit**	**Notes**
Rate of photosynthesis	p	µmol CO_2 m^{-2} s^{-1}	
Rate of transpiration	E	mmol H_2O m^{-2} s^{-1}	
Photosynthetically active irradiation	I	µmol photons m^{-2} s^{-1}	
Efficiency of photosynthesis	b	µmol g m^{-5} s^{-1}	
Stomatal conductance when stomata are fully open	g_{max}	mmol H_2O m^{-2} s^{-1}	
Optimal degree of stomatal opening	u_{opt}	unitless	
CO_2 concentration in ambient air	C_a	g m^{-3}	
Rate of respiration	r	µmol CO_2 m^{-2} s^{-1}	
Temperature	T	K	
State of photosynthetic machinery	S	unitless	
Parameters describing the annual cycle of photosynthesis, estimated using numeric methods (see Hari et al 2017)	a1 … a4		a1 = 10 a2 = 0.065 a3 = 2 a4 = 1.15 * 10^{-7}

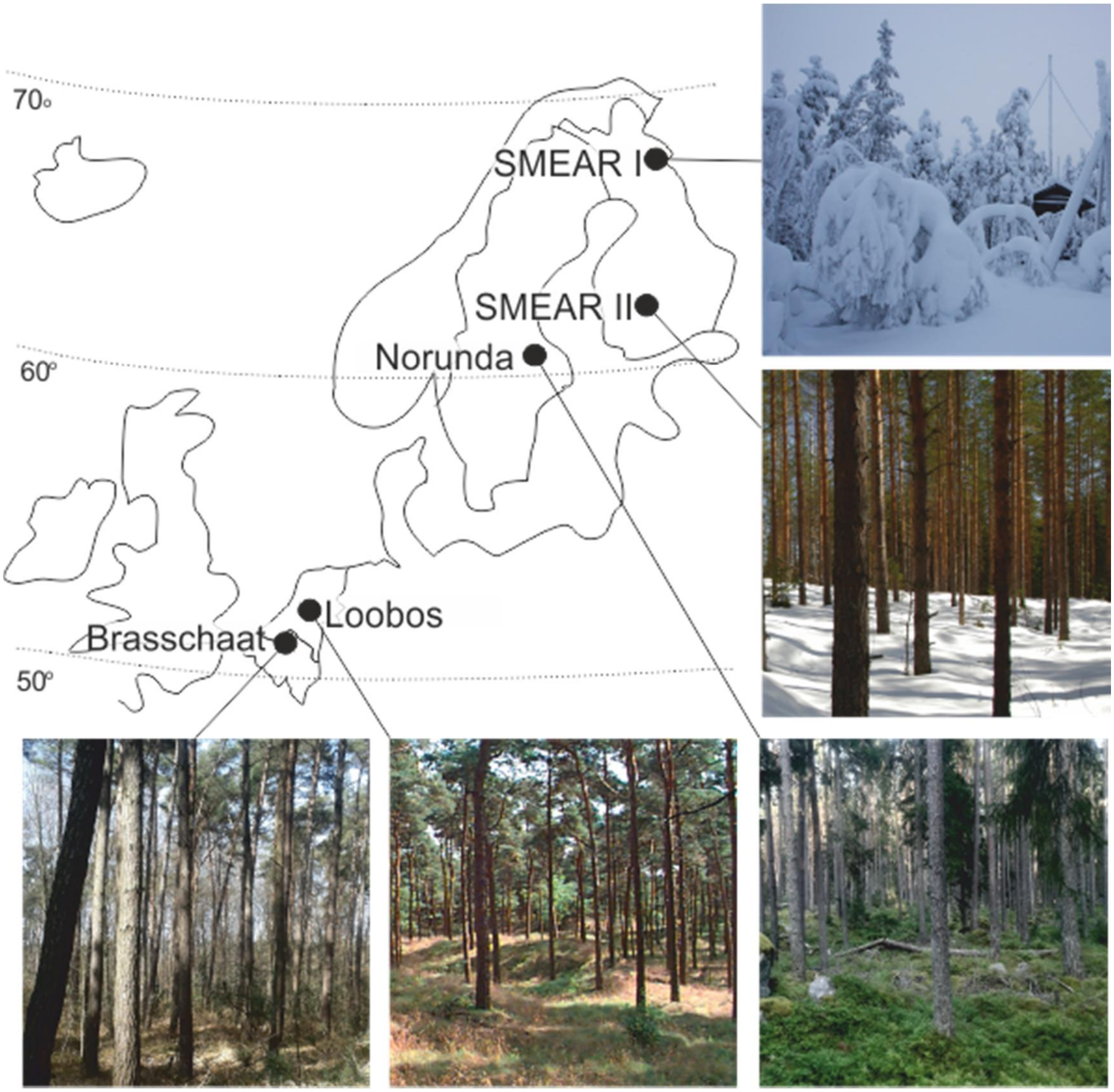

Figure 1. The location of the measuring stations in Europe and photos of the stands. The photo of SMEAR I is taken around Christmas time, SMEAR II early spring, Norunda, Loobos and Brasschaat in summer time.

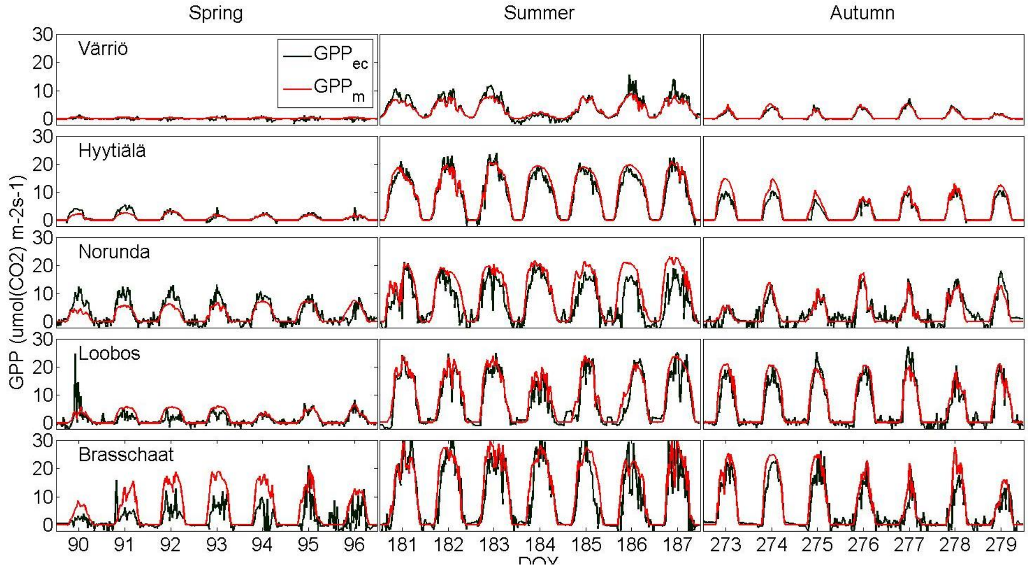

Figure 2. The measured (black) and predicted (purple) photosynthetic CO$_2$ flux (GPP) between forest ecosystem and the atmosphere as function of time in five eddy-covariance measuring sites in Europe during a week in early spring, summer and autumn.

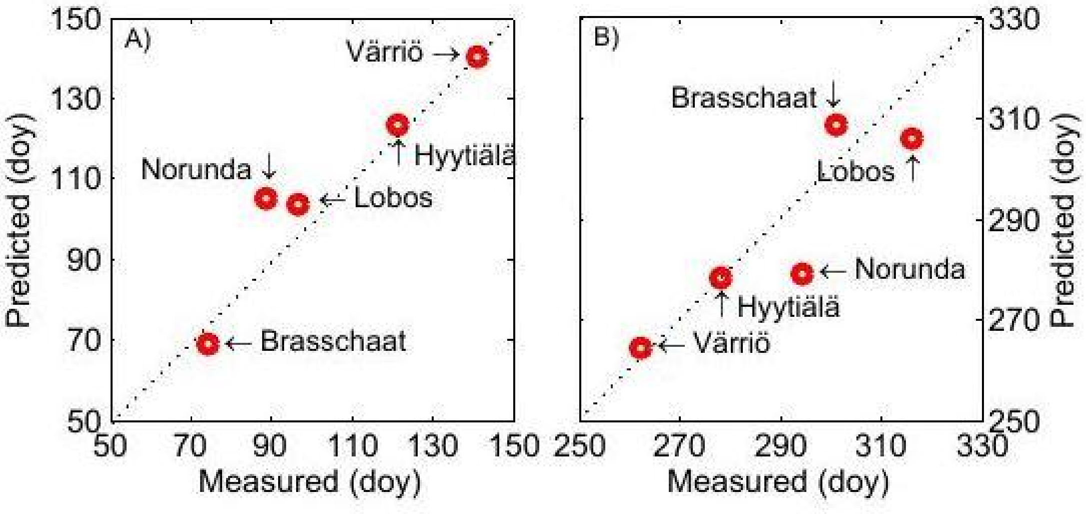

Figure 3. A The relationship between measured and predicted onset and cessation dates of photosynthesis in the five studied ecosystems, B the cessation dates of photosynthesis in the five ecosystems.

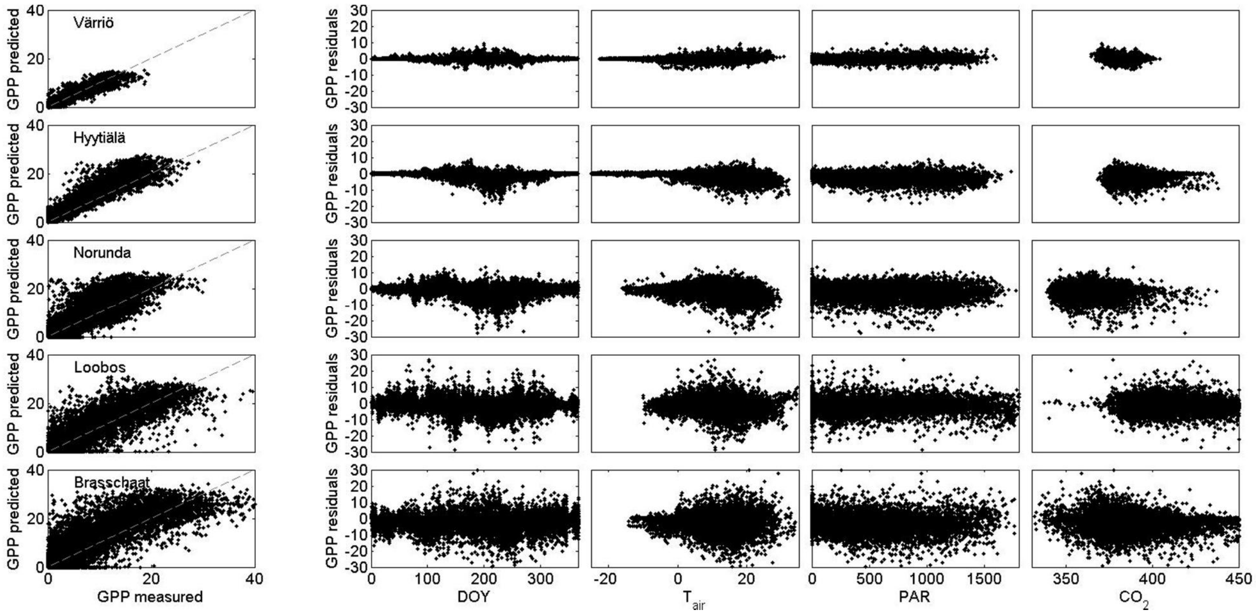

Figure 4. The relationship between measured and predicted gross primary production (the first column). Columns 2-4 present the residuals as function of time, air temperature, photosynthetically active radiation and carbon dioxide concentration.