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

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Abstract. Photosynthesis provides carbon for the synthesis of macromolecules to construct cells during growth. This fact generates the key role of photosynthesis in the carbon dynamics of ecosystems (Taiz et al., 2015) and biogenic CO_2 consumption. The development of eddy covariance measurements of 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 photosynthesis. We then show that 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 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. These stations have provided valuable insights into carbon and energy balances of various ecosystems, but the net fluxes measured with EC do not yield information about the actual processes determining these fluxes. The next important step is to be able to explain 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 fluxes has received strong attention. The statistical approaches connect measured fluxes with environmental factors typically using rather simple 'big-leaf' models whose parameters are determined from ecosystem-scale EC data (Landesberg and Waring, 1997; Peltoniemi et al., 2015). More theoretically driven modeling approaches are based on knowledge of metabolism, and account for the structure of the considered ecosystem. For instance, Farquhar et al. (1980) developed a photosynthetic model 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; Katul et al., 2010; Medlyn et al., 2011). 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-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.

We followed 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). 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 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 Eq. (1). It links the theoretical knowledge and climatic drivers (light,

5   temperature, and CO_2 and water vapour concentration) to photosynthesis.

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

where b is parameter called the efficiency of photosynthesis, g_{max} is parameter introducing stomatal conductance when stomata

10   are fully open and u_{opt} is optimal degree of stomatal opening obtained from as solution of the optimisation problem of stomatal behaviour (Hari et al 2014).

We then analysed the annual cycle of photosynthesis. Importantly, there is a strong annual cycle in the concentrations of active pigments, membrane pumps and enzymes, generating the distinctive annual cycle in photosynthesis of evergreen foliage (Pelkonen and Hari, 1980; Öquist and Huner, 2003; Ensminger et al., 2004). The changing state of the photosynthetic

15   machinery over the course of a year is a characteristic feature of the annual cycle of photosynthesis in coniferous trees. Scots pine has a regulation system that synthetizes and decomposes pigments, membrane pumps and enzymes in the photosynthetic machinery. We introduced 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) describing the behaviour of

20   the state of the photosynthetic machinery Eq. (2).

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

25   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. Our theoretical thinking determines the structure of these two equations.

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

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We estimated the values of the parameters in Eqs. (1) and (2) by analysing shoot-scale measurements of the CO_2 exchange of 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

5   shoot level measured with chambers (Hari et al., submitted manuscript).

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

10   measurements in Värriö, in the behaviour of the photosynthetic CO_2 flux between Scots pine ecosystems and the atmosphere across Europe.

2 Results

The eddy-covariance methodology provides the mean CO_2 flux during some time interval, usually 0.5h. The measured flux combines the photosynthesis of pines and of other vegetation growing on the site and, in addition, the respiration of plants and

15   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 and we call it gross primary production, GPP according to the common practice in the eddy-covariance research.

Applying our equations dealing with the photosynthesis of one shoot to predict photosynthesis at Scots pine ecosystem level

20   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, difference in species, and in extinction of light in the canopy, etc. We expect that 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.

25   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 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 the one we wanted to predict. Thereafter we were able to predict the GPP in the five ecosystems in Europe. We based our prediction utilising the two equations on the measured values of light, temperature

30   and CO_2 and water vapour concentrations done in each site, on the parameter value obtained in the chamber measurement 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. The predictions obtained for all measured Scots pine ecosystems were successful (Fig. 2) in describing the dynamic features of GPP.

The predictions of the daily patterns of measured 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 rapid increase of

5   GPP after sunrise, its saturation in the middle of the day, and its decline when the light intensity is decreasing towards evening. Clouds reduce the light intensity to variable degrees, causing rapid variations in the CO_2 flux (Brasschaat day 186 and 187) and strong reduction in this flux on days with heavy clouds (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 as the moment when the running mean of 14 days of photosynthetic CO_2 flux exceeds 20

10 % of the corresponding running mean in midsummer and the moment of cessation when the running mean of CO_2 flux has declined to 20 % of its summer time value. Our prediction of the onset and cessation moments of photosynthesis in the different measuring sites was quite successful, as the observed and predicted dates of the onset and cessation of photosynthesis were very close to each other at different measurement sites (Fig. 3 panels A and B). Surprisingly, the parameter values in the differential equation dealing with the synthesis and decomposition of the photosynthetic machinery, obtained from chamber

15 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.

Our predictions explain 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. The measuring noise of eddy-covariance measurements is quite large, about 10–30 % (Rannik et al., 2004; Richardson et al., 2006), it therefore dominates

20 the residuals, i.e. the difference between measured and predicted fluxes. We further studied the residuals as function of light, temperature, CO_2 and water vapour concentration (Fig. 4). We detected only minor systematic behaviour in the residuals.

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).

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3 Discussion

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 environmental factors and photosynthetic CO_2 flux of Scots pine ecosystems during a year. Consequently, we are unable to compare our results with results reported in the literature.

30 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 research of carbon budgets of Scots pine 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 change stresses the importance to understand the ecosystem responses to increasing atmospheric CO_2 concentration and temperature. The equations 1 and 2 resulted 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 this temperature increase is smaller than the temperature difference between Värriö and Brasschaat, i.e. about 10 °C. The equations 1 and 2 provide also 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 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 two equations was successful in five Scots pine ecosystems, from northern timberline to Central Europe. Thus, the regularities observed in the chamber measurements in Värriö play a very important role in the photosynthetic CO_2 flux between Scots pine ecosystems and the atmosphere in five stands from arctic Lapland to Central Europe. 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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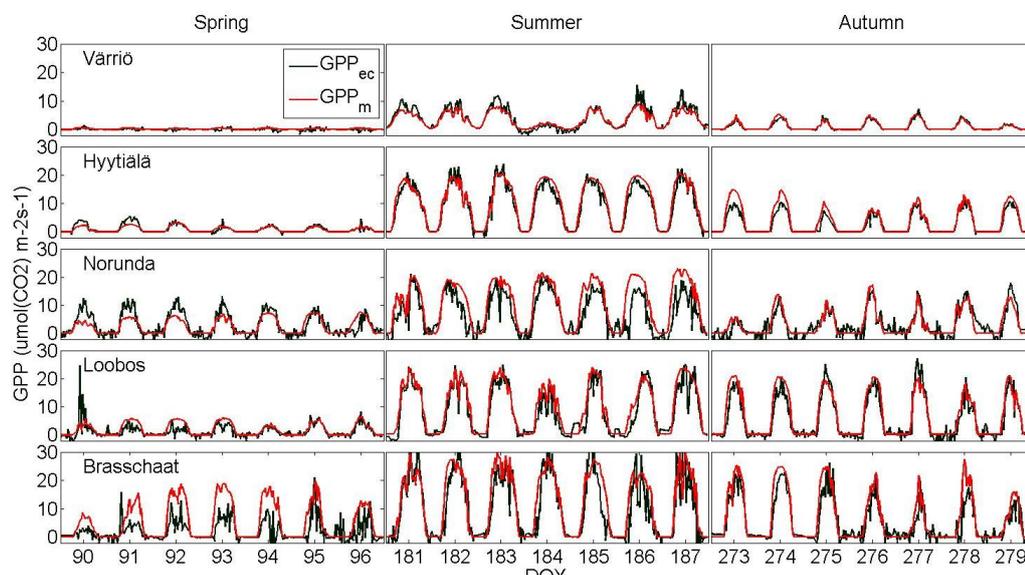
Figure 1. The measured (black) and predicted (purple) photosynthetic CO_2 flux (GPP) between forest ecosystem and the atmosphere as function of time in five eddy-covariance measuring sites in Europe during a week in early spring, summer and autumn.
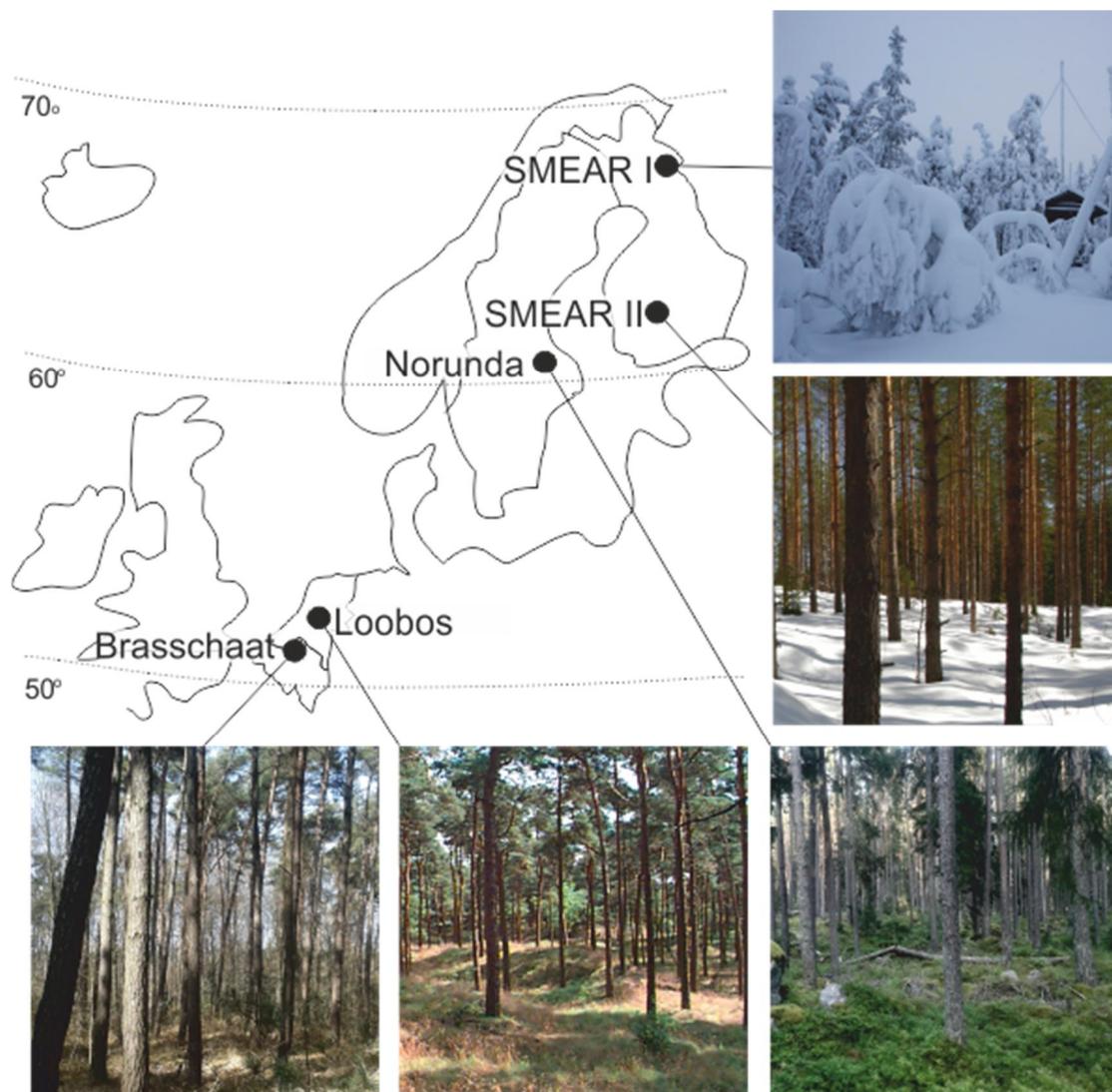
Figure 2. The location of the measuring stations in Europe and photos of the stands. The photo of SMEAR I is taken around Christmas time, SMEAR II early spring, Norunda, Loobos and Brasschaat in summer time.
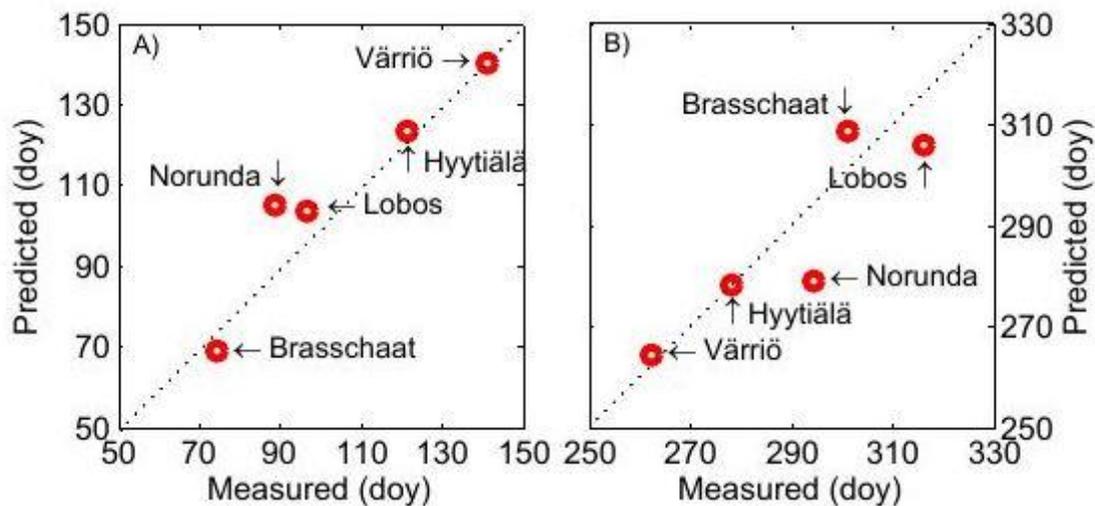
Figure 3. A The relationship between measured and predicted onset and cessation dates of photosynthesis in the five studied ecosystems, B the cessation dates of photosynthesis in the five ecosystems.
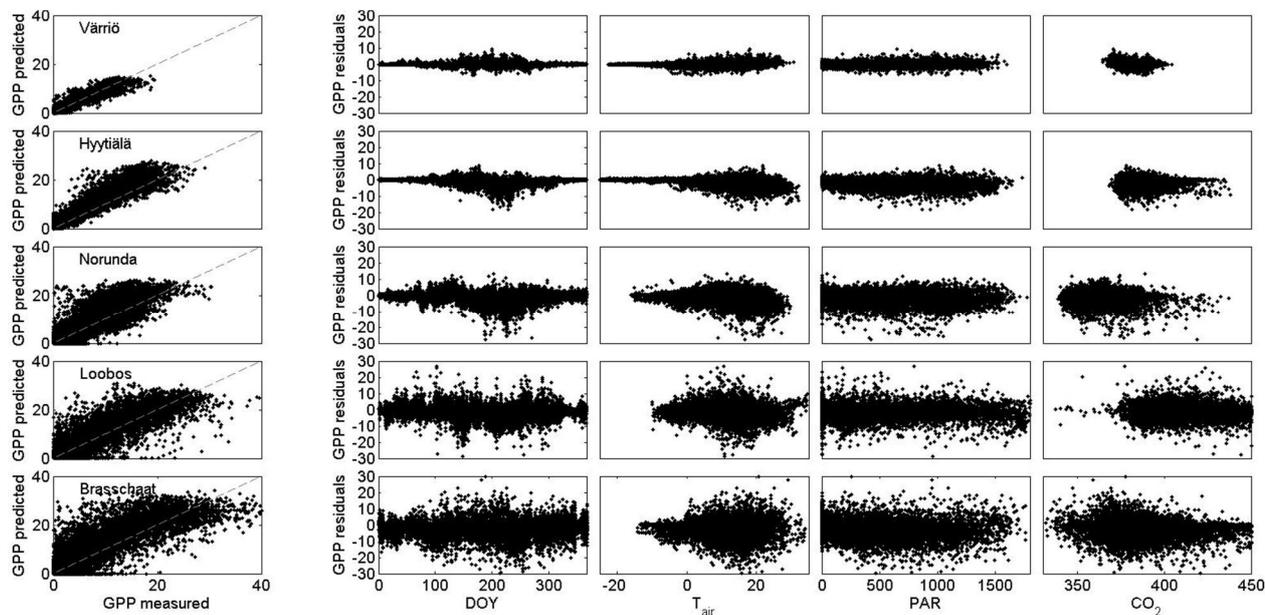
Figure 4. The relationship between measured and predicted gross primary production (the first column). Columns 2-4 present the residuals as function of time, air temperature, photosynthetically active radiation and carbon dioxide concentration.