Intercomparison of methods to estimate GPP gross primary production based on CO₂ and COS flux measurements

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Abstract. Knowing Separating the components of ecosystem scale carbon exchange is crucial in order to develop better models and future predictions of the terrestrial carbon cycle. However, there are several uncertainties and unknowns related to current photosynthesis estimates. In this study, we test the use of evaluate four different methods for quantifying estimating photosynthesis at the ecosystem scale, of which two are based on carbon dioxide (CO₂) flux measurements and two on carbonyl sulfide (COS) flux measurements. The CO₂-based methods use traditional flux partitioning and artificial neural networks to separate the net CO₂ flux into respiration and photosynthesis. The COS-based methods make use of a unique five-year flux data set at a boreal forest and involve two different approaches to determine the leaf-scale relative uptake ratio of COS and CO₂ (LRU), of which one (LRU₂₅) was developed in this study. LRU₁₆ was based on stomatal conductance theories, while the other—a previously tested stomatal optimization theory (CAP), while LRU₁₆ was based on an empirical relation to measured radiation (LRU₁₆)

We found that for the measurement period 2013–2017, the artificial neural networks method gave a GPP estimate very close to that of traditional flux partitioning at all time scales. On average, the COS-based methods gave on average—higher GPP estimates than the CO₂-based estimates on daily (23 and 7 % higher, if using LRU₂₅ or and LRU₁₆ in GPP calculation, respectively) and monthly scales (20 and 3 % higher), as well as a higher cumulative sum over three months in all years (on average 25 and 3 % higher). LRU₂₅ was higher than measured LRU LRU estimated from chamber measurements at high radiation leading to an underestimated GPP during midday. However, in general it compared better with the underestimation of midday GPP. In general, however, use of LRU₂₅ gave closer agreement with CO₂-based methods than estimates of GPP than use of LRU₂₅ based GPP calculations. The applicability of LRU₂₅ in extending to other sites, LRU₂₅ at other measurement sites is potentially better than that of may be more robust than LRU₂₅ since its parameters are based on literature values and because it is based on a physiological model whose parameters can be estimated from simple meteorological measurements;
while the or the literature. In contrast, the empirical radiation relation in LRU_{\text{PAR}} might be may be more site-specific. This, however, this requires further testing at other measurement sites.

1 Introduction

Photosynthetic carbon uptake (described by or gross primary production, GPP) is a crucial part of carbon cycling and removes key component of the global carbon cycle, with the terrestrial ecosystems removing approximately 30% of the annual anthropogenic carbon dioxide (CO₂) emissions from the atmosphere (Luo et al., 2015; Friedlingstein et al., 2020). With the current climatic warming it is has been suggested that both photosynthesis and respiration are increasing, due to the CO₂ fertilization effect and rising temperatures allowing more optimal conditions providing more favourable conditions not only for photosynthesis but also for respiration (Dusenge et al., 2019). However, it is not known at which ratio these two processes are changing and whether they cancel each other out or not, thus the extent to which they offset each other. In addition, there is a seasonal variation in their relative importance, as photosynthesis varies seasonally, with photosynthesis predicted to increase more than respiration in spring, causing leading to greater carbon uptake, while respiration is predicted to increase more than photosynthesis in autumn, causing carbon emissions in the leading to net carbon emission in northern terrestrial ecosystems (Piao et al., 2008). Methods to measure and study photosynthesis and respiration processes individually are thus crucial for future carbon cycle predictions.

Eddy covariance (EC) is widely used globally to measure the biosphere-atmosphere exchange of CO₂ at the ecosystem scale. With EC it is, however, only possible to measure the However, EC only measures net ecosystem CO₂ flux (NEE), which includes contributions from both CO₂ uptake by photosynthesis (GPP) as well as and ecosystem respiration (R). Traditionally, NEE partitioning into GPP and respiration is most commonly done using a method introduced by Reichstein et al. (2005), in which temperature response curves are fitted to nighttime CO₂ flux data (respiration). However, this method is problematic due to the reliance on nighttime EC flux measurements, which are uncertain and often filtered out due to low turbulence conditions and possible advective gas transport (Aubinet, 2008). Partitioning methods that are To address this problem, partitioning methods have been developed based on a combination of nighttime respiration temperature response-temperature responses of respiration (nighttime method) and daytime GPP-radiation response radiation responses of GPP (daytime method) have also been developed in order to not rely on nighttime responses only (Lasslop et al., 2010; Kulmala et al., 2019). Both (Lasslop et al., 2010; Kulmala et al., 2019). However, both the nighttime method and the combination of nighttime and daytime methods, however, assume that the respiratory processes are the same in the daytime and nighttime combined nighttime-daytime method assume that respiratory processes operate in the same way during the day and night, and have uncertainties due to assumptions of functional relationships (Tramontana et al., 2020).

These limitations assumptions lead to uncertainties in the derivation of mechanistically sound descriptions of respiration and its drivers, especially when contributions of partitioning because different biomass compartments to total CO₂ efflux vary across ecosystems and seasonally even within one soil organic matter, roots, stems, branches, foliage could have different drivers and respiration responses even within the same ecosystem (Kolari et al., 2009; Keenan et al., 2019). Recently, there
has been discussion on leaf respiration inhibition under. Leaf respiration during the day may be inhibited by radiation, the so-called Kok effect (Kok, 1949; Heskel et al., 2013; Yin et al., 2020) and Keenan et al. (2019) and Wehr et al. (2016) also suggest that the global GPP estimates also suggest that, as a result, global GPP based on the nighttime method are exaggerated due to this phenomenon has been overestimated. On the other hand, photorespiration, which is an oxidation process competing with carboxylation under radiation, might cancel out the offset inhibition by the Kok effect (Heskel et al., 2013).

One way to address biases related to these uncertainties in flux partitioning is using to use machine learning methods, such as artificial neural networks in separating to separate NEE into respiration and GPP (Tramontana et al., 2020). The benefit of NNc-part advantage of this method is that it requires no predefined knowledge on makes no a priori assumptions about responses to environmental drivers but determines them purely based these based only on data. A pioneering experiment from Desai et al. (2008). In a pioneering study, Desai et al. (2008) attempted to use artificial neural network to emulate the nighttime partitioning method without, but obtained no significant improvements. Recently More recently, Tramontana et al. (2020) proposed a new approach (NNc-part) has been proposed by Tramontana et al. (2020). The proposed method is innovative for the peculiarity of the implemented involving novel methods for implementing the network’s structure and a novel way to infer of inferring GPP and R signals from NEE. Both nighttime and daytime NEE are used for network training, so the dynamics of biophysical processes are accounted for in a comprehensive way.

Another recent development to tackle the GPP problem Yet another approach to addressing uncertainties in GPP estimates is to use proxies for CO2 uptake. One such proxy is carbonyl sulfide (COS), which is a sulfur compound with a tropospheric mixing ratio around of approximately 500 ppt (Montzka et al., 2007). It–While the use of different CO2-based partitioning methods is primarily aimed at more accurate GPP estimation, in contrast the use of COS as a proxy for GPP is aimed at a better process understanding of GPP. COS is mainly produced by oceans and anthropogenic sources (Kettle et al., 2002; Berry et al., 2013; Launois et al., 2015; Whelan et al., 2018) while vegetation is the largest sink (Sandoval-Soto et al., 2005; Blonquist et al., 2011). COS has been suggested-proposed as a proxy for GPP since because it is taken up by plants through the same diffusive pathway as CO2 and transported to the chloroplast surface, where, There it is destroyed by a hydrolysis reaction triggered catalyzed by the enzyme carbonic anhydrase (CA, also located within the cytoplasm (Polishchuk, 2021)), while CO2 continues its journey inside the chloroplast, where it is assimilated in the Calvin cycle (Wohlfahrt et al., 2012). It is assumed that COS is totally destroyed in hydrolysis and thus completely removed by hydrolysis so that there is no back-flux from the leaf to the atmosphere (Protoschill-Krebs et al., 1996). When determining Estimates of GPP from COS flux measurements one needs to take into account use the leaf relative uptake ratio (LRU), that is, the ratio of COS and CO2 deposition rates at the leaf scale. While LRU has been treated either as a global or plant-specific constant value in the past (Asaf et al., 2013; Stimler et al., 2012), recent studies have shown that LRU is a function of solar radiation because CO2 uptake is highly radiation dependent while COS uptake is not (Yang et al., 2018; Kooijmans et al., 2019; Spielmann et al., 2019), and may also vary with vapour pressure deficit (Sun et al., 2018b; Kooijmans et al., 2019). In addition to uncertainties related to LRU, the variation in LRU, COS-based GPP estimates have uncertainty due to ecosystem scale are uncertain because ecosystem-scale COS flux measurements that-typically have a low signal-to-noise ratio and high random uncertainty at 30 min timescale, which reduces although
this is reduced when fluxes are averaged over longer time periods (Kohonen et al., 2020). While the use of different partitioning methods or machine learning in GPP calculation primarily aims at more accurate GPP estimation, the use of COS as a GPP proxy aims at a better process understanding.

In this study, we compare the annual, seasonal, daily and sub-daily variation of i) traditionally partitioned GPP—traditional GPP estimate (GPP\textsubscript{NLR}, NLR referring to non-linear regressions) that is based on a combination of the daytime and nighttime methods, ii) a neural network GPP estimate based on NEE and NN\textsubscript{C–part} (GPP\textsubscript{ANN}), iii) a GPP estimate from based on COS flux measurements using the radiation-dependent LRU function from Kooijmans et al. (2019) (GPP\textsubscript{COS,PAR}) and iv) a GPP estimate from based on COS flux measurements using a new, theory-based method for LRU calculation previously-published stomatal optimization model (CAP) to calculate LRU (GPP\textsubscript{COS,CAP}) in a boreal evergreen needle-leaf forest during years 2013–2017. Our aim is to study potential inconsistencies in diel or seasonal patterns of GPP which could arise from the extrapolation of that may arise from extrapolating nighttime temperature responses to daytime and to discuss the limitations and uncertainties of all four methods. We also make recommendations for improving COS-based GPP estimates.

2 Materials and methods

2.1 Site description

The measurements were done at the Hyytiälä forest Station for Measuring Ecosystem Atmosphere Relations (SMEAR) II measurement site (61°51’N, 24°17’E), where first flux measurements started in 1996 while the forest stand is already more than 50 years old (Hari and Kulmala, 2005). The forest stand is dominated by Scots Pine (\textit{Pinus Sylvestris L.}) with some Norway spruce (\textit{Picea abies L. Karst.}) and deciduous trees (e.g. \textit{Betula sp.}, \textit{Populus tremula}, \textit{Sorbus aucuparia}). The daytime flux footprint covers c. 50 ha area of the forest. The canopy height increased from approximately 18 to 20 m during the measurement period (2013–2017) and the all-sided leaf area index (LAI) was c. 8 m\(^2\) m\(^{-2}\).

2.2 Measurements

2.2.1 Eddy covariance fluxes and environmental measurements

EC measurements were conducted at a 23 m high tower. The setup consisted of a Gill HS (Gill Instruments Ltd., England, UK) sonic anemometer measuring horizontal and vertical wind velocities and sonic temperature, and a quantum cascade laser (QCL; Aerodyne Research Inc., Billerica, MA, USA) for measuring COS, CO\(_2\) and H\(_2\)O mixing ratios at 10 Hz frequency. The setup is described in more detail in Kohonen et al. (2020) and flux data are presented in Vesala et al. (2021). Flux processing was done using EddyUH software (Mammarella et al., 2016) following the methods presented by Kohonen et al. (2020). Fluxes were corrected for storage change and filtered according to friction velocity. Storage change fluxes of COS were calculated from the COS profile measurements in 2015–2017 and from one level concentration measurement concentration measurements at one height in other years, as described in Kohonen et al. (2020), while CO\(_2\) storage change fluxes were calculated from CO\(_2\) concentration profile measurements. Friction velocity filtering
was applied to filter out low turbulence conditions, especially during nighttime (Aubinet, 2008). The friction velocity thresholds were individually determined for COS and threshold was determined from CO\textsubscript{2} fluxes (Papale et al., 2006). and the higher of those thresholds and a threshold of 0.3 m s\textsuperscript{-1} was applied to both fluxes the entire data set to exclude periods of low turbulence. COS flux processing was done otherwise-similarly to CO\textsubscript{2} processing, but time lag and spectral corrections were determined from CO\textsubscript{2} measurements and applied to COS as recommended in by Kohonen et al. (2020). Gap-filling of the COS flux was done using empirical formulas based on photosynthetically active radiation (PAR) and vapor pressure deficit (VPD), described in as described by Kohonen et al. (2020). CO\textsubscript{2} fluxes were gap-filled and partitioned with a procedure using a procedure to be explained in more detail in Sect. 2.3.1.

Environmental measurements used in the study include air temperature \((T_a)\) at 16.8 m (measured with a Pt100 temperature sensor inside a ventilated custom shield), PAR above the canopy (Li-190SZ quantum sensor, LI-COR, Lincoln, NE, USA), relative humidity (RH) at 16.8 m height (Rotronic MP102H, Rotronic Instrument Corp., NY, USA), soil temperature \((T_{soil})\) at 2–5 cm depth (KTY81-110 temperature sensor, Philips, The Netherlands) as a mean of five locations and soil water content (SWC) in the humus layer (Delta-T ML2 soil moisture sensor, Delta-T Devices, Cambridge, UK).

2.3 GPP calculations

In this section, all used GPP calculation methods are explained in detail. This section describes each of the four methods for estimating GPP. Daily average GPP was only calculated if more than 50% of measured the measured 30-min flux data was available for each day, and monthly averages calculated from these data were calculated from the daily means. In Vesala et al. (2022), COS fluxes were found to have 52% data availability on average. While setting a 50% threshold is somewhat subjective, it ensures that the analyzed daily estimates of GPPs reflect measured fluxes rather than the gap-filling procedure. Gap-filled flux data were used in estimating diurnal variation and in calculating the cumulative GPP. All comparisons between the methods were done to used measured (non gap-filled) data only, when both CO\textsubscript{2} and COS flux data were available.

2.3.1 GPP from traditional CO\textsubscript{2} flux partitioning

NEE was partitioned into respiration (R) and GPP\textsubscript{NLR} as

\[
NEE = R - GPP_{NLR}
\]  

(1)

where the GPP model followed the formula

\[
GPP_{NLR} = \frac{\alpha PAR + P_{max} - \sqrt{(\alpha PAR + P_{max})^2 - 4 \Theta PAR \cdot P_{max}}}{2\Theta} \cdot f(T_a)
\]

where \(\alpha\), \(P_{max}\) and \(\Theta\) are fitting parameters and \(f(T_a)\) an instantaneous temperature response that forces GPP to zero when \(T_a < 0 \degree C\) as...
\[ f(T_a) = \frac{1}{1 + e^{2(T_0 - T_a)}} \]

where \( T_0 \) is the inflection point (Kolari et al., 2014).

\[ R = RCQ_{10}^{T_{sa}/10} \]

where \( RC \) is the respiration at a reference temperature (T=0 °C), \( Q_{10} \) is the temperature sensitivity of R and \( T_{sa} \) is the mean of the air temperature at 18 m height and soil temperature at 5 cm depth. Previous studies have shown \( T_{sa} \) has been found to be a good choice as the of respiration driver at Hyytiälä forest in previous studies (Kolari et al., 2009; Lasslop et al., 2012).

When NEE measurements were not available, the GPP model followed the formula

\[ \text{GPP}_{\text{NLR}} = \frac{\alpha \text{PAR} + P_{\text{max}} - \sqrt{(\alpha \text{PAR} + P_{\text{max}})^2 - 4\Theta \text{PAR} \cdot P_{\text{max}}}}{2\Theta} f(T_a) \]

where \( \alpha, P_{\text{max}} \) and \( \Theta \) are fitting parameters and \( f(T_a) \) is an instantaneous temperature response that forces GPP to zero when \( T_a < 0 \) °C, given by

\[ f(T_a) = \frac{1}{1 + e^{2(T_0 - T_a)}} \]

where \( T_0=-2 \) °C is the inflection point (Kolari et al., 2014).

Parameters \( \alpha, P_{\text{max}} \) and \( RC \) were estimated for 11-day 15-day periods while \( Q_{10} \) was estimated from the weighted mean of monthly \( Q_{10} \) values from June–August over several years. Weights were the inverse of the confidence interval of each \( Q_{10} \) estimate. \( \Theta \) was determined as the value that gave the best model fit when the partitioning was run over the during summer months (June–August) over several years (Kulmala et al., 2019). The modeled NEE from Eqs. (3) and (2) was compared with the measured NEE in Fig. B1a.

### 2.3.2 GPP from artificial neural networks

\( \text{GPP}_{\text{ANN}} \) from the data driven model was estimated by applying the \( \text{NN}_{\text{C-part}} \) algorithm (Tramontana et al., 2020). \( \text{NN}_{\text{C-part}} \) is a customized neural network that emulates the bio-physical processes driving both GPP and R at ecosystem spatial scale and was scale and has been applied to several vegetation types distributed globally. The network is composed by two subnetworks: one used to simulate GPP fluxes and the other one for R consists of two subnetworks, which simulate GPP and R, respectively. The two subnetworks are joined together connected in the last node of the overall structure in which, in which the GPP and R signals were are combined to calculate NEE. The subnetwork simulating GPP was composed by GPP subnetwork consists of three layers and it estimated the ecosystem level gross photosynthesis by applying a light use estimates the ecosystem-level
**Gross photosynthesis using a light-use efficiency (LUE) approach:** in particular, instantaneous LUE was estimated by the first two layers while GPP was calculated as the product between LUE and shortwave incoming radiation in the third layer. **NN\textsubscript{C-part} has a hybrid nature and gross photosynthesis is partially constrained by emulating the LUE concept.**

Each subnetwork relies on specific predictors. **Characteristics that distinguish the Distinguishing features of this model** are a) GPP and R derived by other models are not used, b) functional relationships are derived directly from the data and c) the network's weights are tuned by training the machine learning only on NEE measurements. In this experiment we used the same predictors (VPD, incoming shortwave radiation, potential incoming radiation, $T_a$, $T_{soil}$, SWC, wind speed and wind direction) and network structure as applied in by Tramontana et al. (2020). However, to ensure the operability of the method, which is limited by the availability of both predictors and NEE measurements, we set lower requirements concerning for the minimum percentage of measured data for both predictors and half-hourly NEE. Moreover, data from all available years were put together in the same dataset to be used pooled for use in a unique “multi-year” training process. In particular, we applied the following setting: for each year, less than 55% of predictors were gap-filled and at least 365 half-hourly NEE should be measured for both nighttime and daytime. Despite the high percentage of missing data in observations, gaps had generally short duration with limited effects on the uncertainty of predicted outputs. The final GPP\textsubscript{ANN} products were derived by applying trained networks on meteorological inputs, and thus do not include NEE data after network training. The modeled NEE from NN\textsubscript{C-part} was compared with the measured NEE in Fig. B1b.

### 2.3.3 GPP from COS flux measurements and an empirical LRU radiation relation

Based on previous soil chamber measurements it is known that the soil COS flux at Hyytiälä forest site varies only by 1 pmol m$^{-2}$ s$^{-1}$ during the growing season and the diurnal variation is negligible (Kooijmans et al., 2019; Sun et al., 2018a). An average soil flux of -2.7 pmol m$^{-2}$ s$^{-1}$ was thus first subtracted from the quality filtered and gap-filled COS EC fluxes in order to derive the vegetation contribution to the ecosystem COS exchange. GPP was then calculated from the ecosystem COS fluxes (FCOS) using the formula:

$$
GPP_{COS} = \frac{-FCOS}{LRU} \cdot \frac{[CO_2]_a}{[COS]_a}
$$

where $[CO_2]_a$ and $[COS]_a$ denote the atmospheric concentrations of CO$_2$ and COS (in mol m$^{-3}$) at the EC measurement height, measured by the QCL, respectively. **LRU(+)** was calculated as a function of PAR (LRU\textsubscript{PAR}) as described by the empirical equation presented in Kooijmans et al. (2019):

$$
LRU_{PAR} = \frac{607.26}{PAR} + 0.57
$$
This LRU equation was based on field measurements of derived from field chamber measurements (LRU\textsubscript{ch}) of pine branch CO\textsubscript{2} and COS fluxes with two chambers placed at the top of the canopy in 2017 at the same site and were thus independent from the EC flux measurements (Kooijmans et al., 2019). A new theoretical LRU estimate.

### 2.3.4 GPP from COS flux measurements and LRU from stomatal optimization model

Finally, we estimated GPP from Eq. (5) using a new theoretical expression for LRU (LRU\textsubscript{CAP}) was developed based on derived from the stomatal optimization model CAP (Dewar et al., 2018). Full details of the derivation are given in Appendix A. The LRU\textsubscript{CAP} formulation was based on the following general expression for LRU given by Eqs. (10-11) of Wohlfahrt et al. (2012):

$$LRU = \frac{1}{1 - \frac{c_i}{c_a}} \frac{1}{1 + \frac{g^{COS}_i}{g^{COS}_b + g^{COS}_m}} (7)$$

where $g^{COS}_x (x = b, s, m)$ are, respectively, the boundary layer, stomatal and mesophyll conductances for COS, $c_a$ is the atmospheric CO\textsubscript{2} molar mixing ratio (mol mol\textsuperscript{-1}), $c_i$ is the leaf intercellular CO\textsubscript{2} molar mixing ratio (mol mol\textsuperscript{-1}), and the numerical factors 1.21 and 1.14 are the ratios of the conductances of CO\textsubscript{2} to COS for stomata and the boundary layer (Wohlfahrt et al., 2012). If it is assumed that the boundary layer and mesophyll conductances are infinite (as done by Dewar et al. (2018)), Eq. (7) reduces to

$$LRU = \frac{1}{1.21} \left(1 - \frac{c_i}{c_a}\right)^{-1}. (8)$$

An analytical expression for $c_i$ was derived from the stomatal optimization model CAP by Dewar et al. (2018), according to which stomatal conductance maximise leaf photosynthesis, reflecting a trade-off between stomatal limitations to CO\textsubscript{2} diffusion and non-stomatal limitations (NSLs) to carboxylation capacity. The CAP model predicts the value of $c_i$ as an analytical function of various environmental and physiological factors. Inserting this function into Eq. (8), LRU\textsubscript{CAP} can then be expressed as

$$LRU_{CAP} = \frac{1}{1.21} \frac{c_a}{c_a - \Gamma^*} \left(1 + \sqrt{\frac{K_{sl} |\psi_c|}{1.6 g_c VPD \sqrt{1 + \frac{2 \Gamma^* g_c}{\alpha \alpha PAR}}} \right)^{-1}, (9)$$

where $\Gamma^*$ is the CO\textsubscript{2} photorespiratory compensation point (mol mol\textsuperscript{-1}), $K_{sl}$ the soil-to-leaf hydraulic conductance (mol m\textsuperscript{-2} s\textsuperscript{-1} MPa\textsuperscript{-1}), $\psi_c$ is the assumed critical leaf water potential (MPa) at which NSLs reduce photosynthesis to zero, $g_c$ is the carboxylation conductance in the absence of NSLs (mol m\textsuperscript{-2} s\textsuperscript{-1}) and $\alpha$ is the photosynthetic quantum yield (mol mol\textsuperscript{-1}) in the absence of NSLs (Duursma et al., 2008; Dewar et al., 2018). While $\Gamma^*$ and $\alpha$ vary seasonally with temperature, for simplicity we used fixed values representing the growing season averages $50 \times 10^{-6}$ mol mol\textsuperscript{-1} and 0.05 mol mol\textsuperscript{-1}, respectively (Bernacchi et al., 2001; Leverenz and Öquist, 1987; Mäkelä et al., 2008). In addition to PAR (mol m\textsuperscript{-2}s\textsuperscript{-1}) and VPD measurements (mol mol\textsuperscript{-1}), LRU\textsubscript{CAP} requires soil moisture measurements through its dependence on the soil component of $K_{sl}$. All parameter definitions and values are listed in Table 1.
LRU\textsubscript{CAP} is based on a generic physiological model of stomatal function whose predictions have been successfully tested previously (e.g. Lintunen et al. (2020); Salmon et al. (2020); Dewar et al. (2021); Gimeno et al. (2019)). The model parameters are all physiologically meaningful, and can be measured independently or obtained from the literature. This formulation therefore represents a clear advance on previous COS-based methods based on empirical fitting (LRU\textsubscript{PAR}), because it provides a physiological explanation for variations in LRU that may be more robust when extrapolating to other sites.

In addition, LRU\textsubscript{CAP} was calculated using a combination of literature values and fitted parameters by fitting the parameter combinations $X = \frac{|a|}{I_{\text{PAR}}}$ and a more detailed derivation of $Y = \frac{24\Gamma}{g}$ to Eq. (9) is given in the Appendix (Sect. A1 and A2). This analysis was aimed at assessing the parameter sensitivity of LRU\textsubscript{CAP}. While the literature-based parameter values gave $X = 2.5$ and $Y = 0.001$, the fitting values were $X = 2.64$ and $Y = 0.0033$ and gave a slightly better agreement of LRU\textsubscript{CAP} with LRU\textsubscript{ch} (RMSE=1.89, while without fitting RMSE=2.01). However, we emphasise that this fitting procedure was conducted purely in order to assess the model performance and is not a requirement for applying LRU\textsubscript{CAP} in practice when literature-based parameter values are available. Moreover, the results presented in this article are not based on fitted parameter values, but on literature values only.

3 Results and discussion

3.1 Environmental conditions

March 2013 was colder than other years (average -7.0 °C) with also a higher, and also had the highest, average PAR (207.3 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) and lowest soil moisture (0.23 m\(^3\) m\(^{-3}\)) of all years (Fig. 1). May 2017 had high amounts of radiation (monthly average PAR of 478.4 \( \mu \text{mol m}^{-2} \)) and soil temperature was low (3.4 °C), while soil moisture and VPD were at a normal level at 0.28 m\(^3\) m\(^{-3}\). A clear increase in VPD and decrease in soil moisture were seen in August 2013, with soil moisture decreasing from 0.24 in July to 0.19 m\(^3\) m\(^{-3}\) and 0.47 kPa, respectively in August and afternoon median VPD increasing to 1.00 kPa. July 2014 was warmer (19.0 °C) and dryer (VPD 0.88 kPa) than other years but soil moisture remained high at 0.25 m\(^3\) m\(^{-3}\). A clear increase in VPD and a drop in soil moisture were seen in August 2013 and in 2015 when VPD increased from 0.44 in July to 0.62 kPa in August and soil moisture decreased from 0.24 (0.31 in 2015) in July to 0.19 (July to 0.24 in 2015) m\(^3\) m\(^{-3}\) in August in 2013 and afternoon median VPD increased to 1.00 kPa in August 2013. May 2017 had high amounts of radiation (monthly average PAR of 478.4 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) and soil temperature was low (3.4 °C), while soil moisture and VPD were at a normal level at 0.28 m\(^3\) m\(^{-3}\) and 0.47 kPa, respectively. Soil moisture in September–December in 2017 was 10 % higher than other years, while no significant differences between years were found in other environmental variables in late autumn.

3.2 GPP comparison from sub-daily to seasonal scales

Midday GPP\textsubscript{ANN} showed slightly higher midday values than was on average 12 % higher than midday GPP\textsubscript{NLR} during the summer months (May–July) in 2014 and 2017 (Figs. 2,3,4a), opposite to what was found in Tramontana et al. (2020) when comparing the result found by Tramontana et al. (2020) in a comparison of GPP\textsubscript{ANN} to with standard FLUXNET partitioning.
during summer months at multiple sites. The difference between GPP\textsubscript{NLR} and GPP\textsubscript{ANN} during other months was negligible. We tested how the more widely used partitioning method of using only air temperature as the respiration driver, GPP\textsubscript{airT}, (instead of the average of soil and air temperatures) would perform against GPP\textsubscript{NLR} and found that the two methods agreed very well with each other at all time scales studied (Fig. B2). The small differences in the

Table 1. Explanations and sources of the parameters used in the LRU\textsubscript{CAP} formulation for Hyytiäleen forest. \(c_a\) was derived from the measurements in Kooijmans et al. (2019), SWC, PAR and VPD form measurements done in this study. Other values are from Dewar et al. (2018), Duursma et al. (2008) and Nikinmaa et al. (2013). Soil-related values (\(K_{soil,sat}, r_{cyl}, SWC_{sat}\) and \(b\)) are for soil horizon B (which was considered to be representative of the rooting zone), where the SWC measurements were also made. Values measured at the site are written in bold.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Default value or formula and unit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>(c_a)</td>
<td>Atmospheric CO\textsubscript{2} molar mixing ratio</td>
<td>(4.15 \times 10^{-6}) mol mol\textsuperscript{-1}</td>
<td>Measured</td>
</tr>
<tr>
<td>(\Gamma^*)</td>
<td>Photorespiratory compensation point of CO\textsubscript{2}</td>
<td>(50 \times 10^{-6}) mol mol\textsuperscript{-1}</td>
<td>Bernacchi et al. (2001)</td>
</tr>
<tr>
<td>(g_c)</td>
<td>Carboxylation conductance in the absence of non-stomatal limitations</td>
<td>(0.5) mol m\textsuperscript{-2} s\textsuperscript{-1}</td>
<td>Dewar et al. (2018)</td>
</tr>
<tr>
<td>(\psi_c)</td>
<td>Critical leaf water potential</td>
<td>(-2) MPa</td>
<td>Dewar et al. (2018)</td>
</tr>
<tr>
<td>(\alpha)</td>
<td>Photosynthetic quantum yield</td>
<td>(0.05) mol mol\textsuperscript{-1}</td>
<td>Leverenz and Öquist (1987)</td>
</tr>
<tr>
<td>(K_{soil})</td>
<td>Leaf-specific soil-to-leaf hydraulic conductance</td>
<td>(\frac{K_{soil}K_{x}}{K_{soil}+K_{x}}); mol m\textsuperscript{-2} s\textsuperscript{-1} MPa\textsuperscript{-1}</td>
<td>Duursma et al. (2008)</td>
</tr>
<tr>
<td>(K_{x})</td>
<td>Leaf-specific root-to-leaf xylem hydraulic conductance</td>
<td>(0.78 \times 10^{-3}) mol m\textsuperscript{-2} s\textsuperscript{-1} MPa\textsuperscript{-1}</td>
<td>Duursma et al. (2008)</td>
</tr>
<tr>
<td>(K_{soil})</td>
<td>Leaf-specific soil hydraulic conductance</td>
<td>(\frac{R_1}{\text{LAI} \log \left( \frac{r_{cyl}}{r_{root}} \right)}); mol m\textsuperscript{-2} s\textsuperscript{-1} MPa\textsuperscript{-1}</td>
<td></td>
</tr>
<tr>
<td>(k_{soil})</td>
<td>Soil hydraulic conductivity</td>
<td>(k_{soil,sat} \left( \frac{SWC}{SWC_{sat}} \right)^{2b+3}); mol m\textsuperscript{-1} s\textsuperscript{-1} MPa\textsuperscript{-1}</td>
<td>Duursma et al. (2008)</td>
</tr>
<tr>
<td>(k_{soil,sat})</td>
<td>Saturated soil hydraulic conductivity</td>
<td>(5.7) mol m\textsuperscript{-1} s\textsuperscript{-1} MPa\textsuperscript{-1}</td>
<td>Nikinmaa et al. (2013)</td>
</tr>
<tr>
<td>(R_1)</td>
<td>Root length index</td>
<td>(5300) m\textsuperscript{-1}</td>
<td>Measured</td>
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<tr>
<td>LAI</td>
<td>Leaf area index, all-sided</td>
<td>(8) m\textsuperscript{2} m\textsuperscript{-2}</td>
<td>Measured</td>
</tr>
<tr>
<td>(r_{cyl})</td>
<td>Radius of the cylinder of soil accessible to a root</td>
<td>(0.00458) m</td>
<td>Measured</td>
</tr>
<tr>
<td>(r_{root})</td>
<td>Fine root radius</td>
<td>(0.3 \times 10^{-3}) m</td>
<td>Nikinmaa et al. (2013)</td>
</tr>
<tr>
<td>(SWC_{sat})</td>
<td>Saturation soil water content</td>
<td>(0.52) m\textsuperscript{3} m\textsuperscript{-3}</td>
<td>Duursma et al. (2008)</td>
</tr>
<tr>
<td>(SWC)</td>
<td>Soil water content</td>
<td>(m^3 m^\textsuperscript{-3})</td>
<td>Measured</td>
</tr>
<tr>
<td>(b)</td>
<td>Parameter of the soil water retention curve</td>
<td>(4.46)</td>
<td>Duursma et al. (2008)</td>
</tr>
<tr>
<td>(\text{VPD})</td>
<td>Vapor pressure deficit</td>
<td>(\text{mol mol}^{-1})</td>
<td>Measured</td>
</tr>
<tr>
<td>(\text{PAR})</td>
<td>Photosynthetically active radiation</td>
<td>(\text{mol m}^{-2} \text{s}^{-1})</td>
<td>Measured</td>
</tr>
</tbody>
</table>
Figure 1. Median diurnal variation of $T_a$, $T_{soil}$, PAR, SWC and VPD in different months during the measurement period 2013–2017.

diurnal variations of $GPP_{NLR}$ and $GPP_{ANN}$ are thus not due to the chosen choice of temperature measurement as respiration driver. During the measurement period 2013–2017, daily, 30 min, daily and monthly $GPP_{ANN}$ did not differ statistically from $GPP_{NLR}$ statistically (tested with Student’s t-test and the ANOVA test; Fig. B3-B5). However, at on 30 min time scale the $GPP_{ANN}$ was on average 15 % lower than $GPP_{NLR}$. The lower agreement of 30 min $GPP_{ANN}$ and $GPP_{NLR}$ than at longer time scales may have resulted from the NN$_{C-part}$ method restricting $GPP_{ANN}$ to only positive values while $GPP_{NLR}$ may have even negative values due to random noise in the NEE measurements. The relative and absolute differences of $GPP_{ANN}$ to $GPP_{NLR}$ are, however, very small when averaging over longer time periods (Fig. 5).

$GPP_{COS,PAR}$ performed very similarly to $GPP_{NLR}$ especially during morning and early evening (Fig. 2; Figs. 2 and 3), but showed higher midday values than $GPP_{NLR}$, especially during summer months (May–August) in all years. At the daily scale, $GPP_{COS,PAR}$ was on average 23 % higher than $GPP_{NLR}$ (Figs. 4d-e and 5) and also differed from $GPP_{NLR}$
and GPP_{ANN} statistically (p<0.01) as tested with Student’s t-test. on 30 min and daily scales (ANOVA test). On monthly scale, there was no statistical difference to any of the other GPP methods.

To investigate further the causes of the higher GPP_{COS,PAR}, we tried another LRU approach based on a stomatal conductance model, LRU_{CAP} (Sect. ??). LRU_{CAP} uses requires PAR, SWC and VPD as well as ecosystem specific literature values for some parameters as input variables, while In contrast, LRU_{PAR} by Kooijmans et al. (2019) only uses PAR. LRU_{CAP} could potentially better take into account e.g. the therefore takes into account additional effects of drought on stomatal control and air humidity on LRU. In spring, the diurnal variation of GPP_{COS,CAP} closely follows that of GPP_{NLR} and GPP_{ANN} until June (Fig. 2, Figs. 2 and 3). Especially in June and July GPP_{COS,CAP} is lower than the other GPP estimates. At 30 min time scale GPP_{COS,CAP} is on average 12 % lower than GPP_{NLR}, but there is large scatter due to noisy FCOS measurements, as for GPP_{COS,PAR}. However, there is less scatter in GPP_{COS,CAP} beyond GPP_{COS,PAR}, indicating that some of the scatter is due to LRU estimation. At daily scale On daily scales GPP_{COS,CAP} is 7% higher than GPP_{NLR} and at monthly scale on monthly scales the difference decreases to 3%. However, there is no statistically significant difference between the daily 30 min and monthly values of GPP_{NLR} and GPP_{COS,CAP} as tested with Student’s t-test (ANOVA test). The relative and absolute difference of between GPP_{COS,CAP} to and GPP_{NLR} is also mostly lower than that of generally smaller than between GPP_{COS,PAR} to and GPP_{NLR} throughout the year (Fig. 5). In addition, GPP_{COS,CAP} finds reproduces the same two distinctive probability density function peaks as GPP_{NLR} and GPP_{ANN} at 1.7 and 6.6 µmol m^{-2}s^{-1} while GPP_{COS,PAR} finds weaker peaks at 2.4 and 7.4 µmol m^{-2}s^{-1} (Fig. 6). It can be thus said, that In summary, GPP_{COS,CAP} gives a better agreement with traditional GPP_{NLR} partitioning than GPP_{COS,PAR}. However, it was noted that LRU_{CAP} was overestimated higher than LRU_{ch} and LRU_{PAR} at high radiation (PAR > 1000 µmol m^{-2}s^{-1}, Fig. B6a). This may reflect intrinsic differences in the dependence of LRU_{PAR} and LRU_{CAP} on environmental drivers (PAR, VPD, SWC), as both estimates of LRU are based on conditions at the top of the canopy.

LRU_{CAP} was also calculated based on a combination of literature values and fitted parameters the fitted parameters X and Y (Sect. A1) by fitting parameters X = \frac{|\psi_e|}{1.69\alpha} and Y = \frac{21000\alpha}{\alpha} to Eq. (9). This exercise allows for better analysis of the uncertainties of LRU_{CAP} (2.3.4 and A1) in order to assess the sensitivity to parameter values. While literature values would give X = 2.5 and Y = 0.001, the fitting resulted in fitting gave X = 2.64 and Y = 0.0033 and a slightly better agreement of LRU_{CAP} with measured LRU (RMSE=1.89, while without fitting RMSE=2.01). While Thus, while X was close to its literature value, Y was estimated three times higher. This mismatch suggests there may be scope for further model improvement, such as the inclusion of dark respiration and/or finite mesophyll conductance in the LRU_{CAP} model. However, as the difference between fitted LRU_{CAP} and literature-based LRU_{CAP} with only literature values (statistical significance tested with Student’s t-test, p<0.01) was not large, with a median difference of 4 %, and the applicability of the model without fitting is better, we decided to use the literature value-based literature-based parameterisation of LRU_{CAP} in this study, without fitting to measured LRU_{LRU_{ch}}.

LRU_{CAP} was also calculated assuming finite mesophyll conductance as a test further comparison (Sect. A2). The agreement of this method was better than assuming infinite mesophyll conductance at high PAR, but worse at low PAR (Fig. B6d), very similar to the results from Maignan et al. (2021), who modelled LRU at Hyytiälä using the ORCHIDEE model. This version
of \( \text{LRU}_{\text{CAP}} \) was also fitted to measured LRU in terms of parameters \( X \) and \( Y \) (Sect. A2) to make the low PAR \( \text{LRU}_{\text{CAP}} \) better, which resulted in \( X = 3.45 \) and \( Y = 0.0057 \), both higher than their expected literature values. We thus concluded that the assumption of infinite \( g_m \) is more valid gives an estimate that is closest to \( \text{LRU}_{\text{ch}} \), although the assumption in itself is physiologically unrealistic. Kooijmans et al. (2019) found that internal conductance (a combination of mesophyll conductance and biochemical reactions) might limit leaf-scale FCOS during daytime. We find a better agreement of \( \text{LRU}_{\text{CAP}} \) with measured \( \text{LRU}_{\text{ch}} \) if \( g_m \) is assumed infinite, but there is a mismatch at high PAR, supporting the possibility that \( g_m \) might indeed be a limiting factor under high radiation. In \( \text{CAP} \), infinite or finite \( g_m \), represent two contrasting hypotheses, in which NSLs act either entirely on photosynthetic capacity, or entirely on \( g_m \), respectively. In reality, NSLs may act on both photosynthetic capacity and \( g_m \), with one or the other effect being dominant depending on environmental conditions. The contrasting abilities of each hypothesis to explain \( \text{LRU}_{\text{ch}} \) at low vs. high light might be explained by a shift in the action of NSLs from the photosynthetic capacity to \( g_m \) as light increases. However, verifying this possibility lies beyond the scope of the present study.

All \( \text{We calculated the cumulative GPP estimates over May–July (Table 2) were about half of the yearly GPP reported previously (Lagergren et al., 2008; Ilvesniemi et al., 2009; Kolari et al., 2009; Suni et al., 2003), since we did not measure GPP over the whole growing season (that lasts c. 30 weeks) but only 13 weeks around the peak growing season for each year. Cumulative GPP}_{\text{COS,PAR}} \) was (on average 25 %) higher than cumulative GPP}_{\text{NLR}} \) in all studied years. This is higher than the 4.3 % difference reported in Spielmann et al. (2019) and 3.5 % agreement reported in Commane et al. (2015). Cumulative In contrast, cumulative GPP}_{\text{COS,CAP}} \) on the other hand varied from 17 % higher in 2014 to 15 % lower in 2015 being on average, and on average was only 3 % higher than cumulative GPP}_{\text{NLR}} \). Cumulative GPP}_{\text{ANN}} \) varied from 10 % higher in 2014 to 9 % lower in 2016 than GPP}_{\text{NLR}} \), on average being and on average was 0.1 % lower than GPP}_{\text{NLR}} \). As stated above, overall GPP}_{\text{ANN}} \) was closest to GPP}_{\text{NLR}} \) from the three out of the three other GPP estimates. GPP}_{\text{COS,CAP}} \) was closer to both of the CO2-based GPP estimates than GPP}_{\text{COS,PAR}} \). However, at high PAR, \( \text{LRU}_{\text{COS,CAP}} \) was overestimated in comparison to observations higher than chamber-based measurements, leading to underestimated GPP. Still, lower GPP. Nevertheless, no firm conclusions can be drawn as the LRU observations only cover measurements at the top of the canopy, and may not reflect LRU over the whole canopy.

It has been suggested that, due to the Kok effect, leaf respiration is inhibited under radiation (Kok, 1949). This inhibition has been estimated to be approximately 13 % in the evergreen needle-leaf forests during summer (Keenan et al., 2019). Isotopic studies measuring the Measurements of CO2 isotope fluxes have come to support the conclusion that, due to the Kok effect, the traditional GPP from GPP from traditional CO2 flux partitioning using the nighttime method is overestimated and isotopic flux measurements support this statement (Wehr et al., 2016). However, the ecosystem respiration at the Hytytiäli forest site is dominated by soil respiration (Ilvesniemi et al., 2009), which could limit the importance of so that the Kok effect may be of limited importance in this ecosystem (Keenan et al. (2019); Yin et al. (2020)). Reduced leaf respiration under radiation would be visible as a break point around the compensation point with a change of the slope of NEE against radiation. However, such a break point was not detected in our observations, as is demonstrated in Fig. B7. It is thus not expected that independent GPP estimates in Hytytiäli would necessarily result in lower GPP than the traditional methods. Moreover, as demonstrated in
Figure 2. Median diurnal variation of traditionally partitioned GPP (GPP\(_{\text{NLR}}\), purple line), GPP from artificial neural networks (GPP\(_{\text{ANN}}\), pink line), GPP from COS flux measurements with LRU determined according to Kooijmans et al. (2019) (GPP\(_{\text{COS,PAR}}\), dark blue line) and GPP from COS flux measurements using a new approach for LRU (Sect. ??, GPP\(_{\text{COS,CAP}}\), light blue line) in different months during the measurement period 2013–2017. Averaging was done to the same data points and only months with more than 55 % of data coverage were included.

Tramontana et al. (2020), the Tramontana et al. (2020) showed that uncertainties and biases in NEE (and COS flux) measurements exceed those resulting from the possible Kok effect.

3.3 GPP responses to environmental conditions

All four GPP estimates responded similarly to environmental forcing (PAR, \(T_a\), VPD) both in spring and summer (Fig. 7). In spring, all GPP estimates increased with increasing radiation levels, while in summer a saturation point was found at \(\text{PAR}>500\)
Figure 3. Diurnal variation of the difference of GPP_{ANN} (pink), GPP_{COS,PAR} (dark blue) and GPP_{COS,CAP} (light blue) to the reference GPP_{NLR} in different months during the measurement period 2013–2017. Averaging was done to the same data points and only months with more than 55 % of data coverage were included.

$\mu$mol m$^{-2}$s$^{-1}$, that could be linked to VPD limitation on stomatal conductance in the afternoon (Kooijmans et al., 2019). GPP_{COS,PAR} was higher than GPP_{COS,CAP} at PAR>400 $\mu$mol m$^{-2}$s$^{-1}$ while at low PAR values they agreed well with each other both in spring and summer, as well as with GPP_{NLR} and GPP_{ANN}. GPP_{COS,PAR} thus has a stronger radiation response than the other GPP estimates. A similar PAR response was found in Spielmann et al. (2019), who studied GPP_{COS,PAR} with a traditional GPP partitioning method in four different sites in Europe. Although GPP_{COS,CAP} agrees well with both GPP_{NLR} and GPP_{ANN} at high PAR, it is likely underestimated due to overestimated high LRU_{CAP} at high PAR (Fig. B6).

In spring, increasing air temperature increased all GPP estimates similarly until $T_a$ reached 17°C. However, again GPP_{COS,PAR} was higher than other GPP estimates. In summer, air temperature did not have a notable effect on any GPP estimate. Responses
Figure 4. Scatter plots of GPP\text{ANN}, GPP\text{COS,PAR} and GPP\text{COS,CAP} against GPP\text{NLR} in 30 min, daily and monthly time scales. The color of data points in 30 min and daily scatter plots indicate the data density, lighter colors indicating higher point density than dark.

to VPD were similar for each GPP estimates both in spring and summer. In spring, decreasing air humidity (increasing VPD) was increasing associated with increased GPP until VPD>0.7 kPa after which VPD did not have an effect—had little or no effect. The apparent increase in GPP with VPD in spring may be caused by the correlation of $T_a$ with VPD, coinciding with the start of the growing season, as the trees are not water-limited after snow melt. In summer, dryness started to limit GPP at VPD>1 kPa. We found that similar to PAR and $T_a$ responses, GPP\text{COS,PAR} was higher than other GPP estimates at low VPD values, but decreased to similar levels at high VPD (1 kPa) both in spring and summer.
**Figure 5.** Relative (a) and absolute (b) difference of daily GPP\textsubscript{ANN} (pink), GPP\textsubscript{COS,PAR} (dark blue) and GPP\textsubscript{COS,CAP} (light blue) to GPP\textsubscript{NLR} in different months, averaged over the whole measurement period 2013–2017. Bars represent the median difference, and whiskers show the 25th and 75th percentiles. Numbers on top of the bars indicate how many daily flux data points have been used for calculating the medians. **All medians have been calculated using the same number of data points.**

**Table 2.** Cumulative GPP (gC m\textsuperscript{-2}) over May–July with different GPP estimates. All sums are calculated from same data coverage and the fraction of gap-filled flux data (CO\textsubscript{2} flux for GPP\textsubscript{NLR}, COS flux for GPP\textsubscript{COS,PAR} and GPP\textsubscript{COS,CAP}) is presented in parentheses. GPP\textsubscript{ANN} does not include gap-filled NEE data, since it is based on meteorological variables. *In 2015, the cumulative sum covers only July.

<table>
<thead>
<tr>
<th>Year</th>
<th>GPP\textsubscript{NLR}</th>
<th>GPP\textsubscript{ANN}</th>
<th>GPP\textsubscript{COS,PAR}</th>
<th>GPP\textsubscript{COS,CAP}</th>
</tr>
</thead>
<tbody>
<tr>
<td>2013</td>
<td>481 (0.16)</td>
<td>473</td>
<td>597 (0.28)</td>
<td>510 (0.28)</td>
</tr>
<tr>
<td>2014</td>
<td>294 (0.20)</td>
<td>324</td>
<td>414 (0.24)</td>
<td>343 (0.24)</td>
</tr>
<tr>
<td>2015</td>
<td>193 (0.23)*</td>
<td>188*</td>
<td>212 (0.31)*</td>
<td>165 (0.31)*</td>
</tr>
<tr>
<td>2016</td>
<td>623 (0.40)</td>
<td>565</td>
<td>722 (0.43)</td>
<td>599 (0.43)</td>
</tr>
<tr>
<td>2017</td>
<td>387 (0.35)</td>
<td>399</td>
<td>522 (0.34)</td>
<td>428 (0.34)</td>
</tr>
</tbody>
</table>
Figure 6. Distribution (bars) and probability density functions (lines) of daily average (a) $GPP_{NLR}$, (b) $GPP_{ANN}$, (c) $GPP_{COS,PAR}$ and (d) $GPP_{COS,CAP}$. All probability density functions are combined in (e) for better comparison.

Wohlfahrt et al. (2018) used FCOS to determine whether a reduction in GPP during a heatwave is due to diffusional or biochemical limitations, because FCOS tracks the diffusional limitations only while CO$_2$ flux is a combination of both. As we did not observe drought or heatwaves in Hyytiälä during the measurement period, we cannot assess the effects of drought to $GPP_{COS,PAR}$ or $GPP_{COS,CAP}$. We can, however, see that $GPP_{COS,PAR}$ gives higher GPP at low VPD than the CO$_2$-based methods, as does $GPP_{COS,CAP}$ in spring (Fig. 7). This may indicate that something is limiting the photosynthesis reaction (e.g. biochemical limitations in CO$_2$ assimilation) even though the diffusion into the leaf is not limited.
Figure 7. Responses of the different GPP estimates (GPP\textsubscript{NLR} (purple), GPP\textsubscript{ANN} (pink), GPP\textsubscript{COS,PAR} (dark blue) and GPP\textsubscript{COS,CAP}, light blue) to environmental parameters – photosynthetically active radiation (a,d), air temperature (b,e) and vapor pressure deficit (c,f) – in spring (a–c) and summer (d–f). Data are binned to 12 equal sized bins (same number of data points in each bin) and all GPPs have the same data coverage. Only measured (non-gap-filled) 30 min flux data was used and GPP was filtered to include only PAR>700 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in responses to \( T_a \) and VPD to avoid simultaneous correlation with PAR.
3.4 Uncertainties and limitations of the GPP methods

Because GPP\textsubscript{ANN} is purely based on data, it has high sensitivity to the uncertainty in the input data. Moreover, it is sensitive to missing data especially in the case of long data gaps (Tramontana et al., 2020). The method also requires large data sets for training NN\textsubscript{C-part}, not which may not be available at all measurement sites. However, GPP\textsubscript{ANN} does not require prescribed relationships of GPP to environmental data making it an attractive method for sites with good data availability.

GPP\textsubscript{COS,PAR} uses an empirical PAR relation that is based on measurements done at Hyytiälä forest. This relation should be tested against branch scale COS and CO\textsubscript{2} flux measurements at other sites, as a different PAR relation was found in Yang et al. (2018) and it is not known if this relation holds elsewhere. While the LRU\textsubscript{PAR} function is simple, and in that sense thereby attractive, it does not take into account e.g. stomatal regulation during drought or the effects of non-stomatal limitations on photosynthesis. Moreover, as an empirical fit, being an empirical model, it does not provide a process-based understanding for LRU. While the results of GPP\textsubscript{COS,PAR} are promising, we observed a difference similar to what was found in Kooijmans et al. (2019) and found a 25% difference in midday GPP during summer, similar to that found by Kooijmans et al. (2019). We did not find as good agreement with CO\textsubscript{2}-based GPP estimates as Asaf et al. (2013), who found an agreement within 15% between these two methods using a constant LRU of 1.6 in Mediterranean pine forests and crop fields. However, they also reported higher GPP\textsubscript{COS} assumed to be related to soil COS uptake, which was not measured or taken into account in GPP calculations in their study. In our study, we have subtracted an average measured soil flux (Sun et al., 2018a) from the ecosystem COS uptake. As the diurnal variation in soil COS flux was small (less than 1 pmol m\textsuperscript{-2}s\textsuperscript{-1}) throughout the season, so-averaging did not make a large difference, and thus soil does not explain the differences found here. However, as soil COS flux measurements are not necessarily available at all sites, this may be one source of uncertainty in wider application. Yang et al. (2018) studied COS flux components and GPP\textsubscript{COS} in a Mediterranean citrus orchard and found GPP\textsubscript{COS} to be on average 7% lower than traditionally partitioned GPP. They also presented a light-dependent and seasonally varying LRU which, however, could not be applied to Hyytiälä COS fluxes due to the very different ecosystem types studied, indicating that the PAR responses may differ between ecosystems.

GPP\textsubscript{COS,CAP} could be more applicable at other sites than GPP\textsubscript{COS,PAR} due to the use of only literature because it is based on a generic physiological model of stomatal behaviour, which requires only literature-based parameter values and simple meteorological variables in LRU\textsubscript{CAP} without requiring fits to measured LRU as inputs. However, as for LRU\textsubscript{PAR}, LRU\textsubscript{CAP} should also be tested at other sites as well against measured LRU\textsubscript{ch} to verify its applicability at other ecosystems. Moreover, this version of LRU\textsubscript{CAP} assumes infinite mesophyll conductance, which may be a limiting factor of the method. We also provide a while giving reasonable results in comparison with LRU\textsubscript{ch}, is clearly physiologically unrealistic. The formulation of LRU\textsubscript{CAP} with finite \( g_m \) which was not comparable to measured LRU\textsubscript{ch} did not compare as well with LRU\textsubscript{ch} at Hyytiälä forest, but could be so (RMSE=2.58, median difference to LRU\textsubscript{ch}, 22%), especially during low light conditions, but may compare better at other measurement sites.
One source of uncertainty in both of the LRU approaches is that they are based on measurements of GPP estimates based on LRU_{CAP} and LRU_{PAR} is that both LRU predictions are calculated from radiation measurements at the top of the canopy, where there is no foliage blocking the incoming radiation. shading by foliage, although the theoretical dependence of LRU_{CAP} on radiation is more generally applicable throughout the canopy. The branch chamber measurements (which the parameterized on which the empirical LRU_{PAR} function is based) were done) were also made at the top of the canopy and the LRU_{CAP} model is also based on top of the canopy. The measured needles were thus well-adjusted to high radiation conditions and the radiation measurements used in both LRU calculations are also only from above the canopy. Therefore, we did not take into account the light penetration and scatter scattering through canopy. However, the needles and leaves within the canopy are also well adjusted to low light conditions and may be more efficient with their stomatal control in varying light conditions than the needles on top of the canopy. Thus, we do not assume this to be a large source of uncertainty.

### 4 Conclusions

Daily GPP_{ANN} did not statistically differ statistically from daily GPP_{NLR}, and differences were very small also in the also very small on sub-daily and seasonal scales. We found that time scales, GPP_{COS,PAR} was in general higher than GPP_{NLR} at all time scales studied, including a cumulative GPP estimate the estimate of cumulative GPP over a three-month period during the peak growing season. Instead, a better agreement was found between the newly introduced GPP_{COS,CAP} and In contrast, GPP_{COS,CAP}, a new method based on stomatal optimization theory, gave better agreement with GPP_{NLR} at all time scales. GPP_{COS,CAP} was also less scattered noisy (scattered) at 30 min time scale scales than GPP_{COS,PAR}. Moreover, the new The LRU_{CAP} function provides a new theoretical formulation theoretical underpinning for COS-based GPP estimates that can be used at other measurement locations as well, ideally without requiring additional branch chamber measurements. This vast improvement from the represents a significant improvement on previous LRU functions that are based on site-specific empirical fits. However, the LRU_{CAP} model still overestimates LRU at high radiation, when compared to LRU observations at the top of the canopy, leading to an underestimated a lower midday GPP_{COS,CAP} at midday, especially in summer. This discrepancy may result from the assumption of infinite mesophyll conductance, or the lack of dark respiration in the CAP stomatal optimization model, on which LRU_{CAP} is based. All GPP estimates were close to values reported earlier for Hyytiälä. Both COS-based GPP estimates suggest a higher GPP than the CO₂-based methods at on longer time scales. The new LRU_{CAP} model development would benefit from further testing at other measurement sites with COS and CO₂ branch flux measurements, including measurements inside the canopy for better canopy-integrated LRU estimates. The COS-based GPP estimates provide an opportunity for better process-based understanding of photosynthesis, rather than a method applicable everywhere, since the Although COS flux measurements are noisier, expensive and more difficult than those of CO₂, they provide an opportunity for better process-based understanding of photosynthesis, in comparison with more traditional CO₂-based estimates of GPP. In addition to COS, other proxies, such as solar induced fluorescence and isotopic flux measurements should be tested simultaneously to properly investigate their deficiencies and advantages in estimating GPP and processes underlying photosynthesis.
Data availability. Environmental data used in the study are available in the AVAA – Open research data publishing platform (https://smear.avaa.csc.fi/). The metadata of the observations are available via the Etsin service. Flux data will be published in a public repository before publication.
Appendix A: LRU predicted by the CAP stomatal optimization model

A1 LRU_{CAP} assuming infinite mesophyll conductance

The general expression for the leaf relative uptake ratio (LRU) according to Wohlfahrt et al. (2012) is derived from the diffusion laws for COS and CO₂ (Wohlfahrt et al., 2012) is

\[
\text{LRU} = \frac{1}{1 - \frac{c_i}{c_a}} \left(1 - \frac{c_i}{c_a}\right)^{-1} = \left(1 + \frac{g_b^{\text{COS}}}{g_{b_m}^{\text{COS}}} + \frac{g_{s_m}^{\text{COS}}}{g_c^{\text{COS}}} \right)^{-1}.
\]

(A1)

where \(g_x^{\text{COS}}(x = b, s, m)\) are the boundary layer, stomatal and mesophyll conductances for COS, respectively, \(c_a\) is the atmospheric, and \(c_i\) the leaf intercellular CO₂ molar mixing ratio ratios (mol mol\(^{-1}\)), respectively, and the numerical factors 1.21 and 1.14 are the ratios of the conductances of CO₂ to COS for stomata and the boundary layer (Wohlfahrt et al., 2012), respectively.

If it is assumed that boundary layer and mesophyll conductances are infinite, Eq. (A1) reduces to

\[
\text{LRU} = \frac{1}{1.21} \left(1 - \frac{c_i}{c_a}\right)^{-1} = \frac{1}{1.21} \frac{c_a}{c_a} \frac{1 - \hat{c}_i}{\hat{c}_a - 1}.
\]

(A2)

where \(\hat{c}_i = c_i - \Gamma^*\), \(\hat{c}_a = c_a - \Gamma^*\) and \(\Gamma^*\) is the photorespiratory compensation point of CO₂ (mol mol\(^{-1}\)). We derived \(c_i\) was found from a from the CAP stomatal optimization model in which the CAP optimization hypothesis is applied to the bi-substrate photosynthesis model as in Dewar et al. (2018). The bi-substrate (Dewar et al., 2018), according to which stomatal conductance adjusts to maximise the rate of leaf photosynthesis (\(A\)) through a trade-off between stomatal and non-stomatal limitations. Our photosynthesis model is closely based on the one presented by Thornley and Johnson (1990) in based on that of Thornley and Johnson (1990) (their Eq. (9.12)). The CAP solution for stomatal conductance (Dewar et al., 2018) predicts modified to include non-stomatal limitations (NSLs):

\[
\frac{\hat{c}_i}{c_a} A = \frac{1}{1 + \beta} \left(1 - \frac{\psi_{\text{leaf}}}{\psi_c}\right) \frac{\alpha Q g_c (c_i - \Gamma^*)}{\alpha Q + g_c (c_i + \Gamma^*)}.
\]

(A3)

where

\[
\beta = \sqrt{\frac{1.6D}{K_{sl}|\psi_c|} \left(1 + \frac{2\Gamma^*}{\alpha Q}ight}^{-1},
\]

where \(D\) is vapor pressure deficit (VPD), \(\alpha\) is the photosynthetic quantum yield (mol mol\(^{-1}\) \(K_{sl}\) is the leaf-specific soil-to-leaf hydraulic conductance in the absence of NSLs, \(Q\) (mol m\(^{-2}\) s\(^{-1}\)) is photosynthetically active radiation (PAR), \(g_c\) (mol m\(^{-2}\) s\(^{-1}\) MPa) is the initial slope of the \(A - c_i\) response curve in the absence of NSLs, \(\Gamma^*\) (mol mol\(^{-1}\)) \(\psi_c\) is the assumed critical is the photorespiratory CO₂ compensation point, \(\psi_{\text{leaf}}\) (MPa) is the leaf water potential and \(\psi_c\) (MPa) at
which non-stomatal limitations (NSLs) is the critical leaf water potential at which NSLs reduce photosynthesis to zero. $g_s$ is the carboxylation conductance in the absence of NSLs (mol m$^{-2}$ s$^{-1}$), $\alpha$ is the photosynthetic quantum yield. In Eq. (A3), NSLs are represented as an apparent downregulation of the $A - c_i$ response curve by a factor that decreases with decreasing leaf water potential, as has been observed in numerous experiments (e.g. Lintunen et al. (2020); Salmon et al. (2020)). Consequently, as stomatal conductance increases there is a trade-off between increased CO$_2$ supply and increased NSLs, such that $A$ has a maximum at some optimal value of stomatal conductance.

We used Eq. (A3) rather than the Farquhar photosynthesis model (Farquhar et al., 1980) because, in the latter, the abrupt switch from Rubisco- to electron transport limitation introduces artificial discontinuities in the CAP solution for optimal stomatal conductance (Dewar et al., 2018), whereas in Eq. (A3) there is a smooth transition from CO$_2$- to light limitation and no such discontinuities occur. The parameter $g_c$ is equivalent to $V_{cmax}/(K_m + \Gamma^*)$ in the Farquhar model.

The CAP solution for optimal stomatal conductance (Dewar et al., 2018) predicts that

$$\frac{c_i - \Gamma^*}{c_g - \Gamma^*} = \frac{1}{1 + \beta},$$

(A4)

where

$$\beta = \sqrt{\frac{1.6D}{K_{sl}|\psi_c|} \left(\frac{1}{g_c} + \frac{2\Gamma^*}{\alpha Q}\right)^{-1}},$$

(A5)

in which $D$ is vapor pressure deficit (VPD; mol mol$^{-1}$) in the absence of NSLs and $Q$ is the photosynthetically active radiation (PAR); and $K_{sl}$ is the leaf-specific soil-to-leaf hydraulic conductance (mol m$^{-2}$s$^{-1}$). Substituting Eqs. (A4) and (A5) and the definition of $c_a$ into Eq. (MPa$^{-1}$). Writing Eq. (A2) gives

in the equivalent form

$$LRU = \frac{1}{1.21} \frac{c_a}{c_g - \Gamma^*} \left(1 - \frac{c_i - \Gamma^*}{c_a - \Gamma^*}\right)^{-1}$$

(A6)

and substituting the CAP prediction from Eqs. (A4) and (A5) then gives

$$LRU_{CAP} = \frac{1}{1.21} \frac{c_a}{c_g - \Gamma^*} \left(1 + \frac{1}{1.21} \frac{c_a}{c_g - \Gamma^*}\right) \left(1 + \frac{K_{sl}|\psi_c|}{1.6Dg_c} \frac{1 + \frac{2\Gamma^*g_c}{\alpha Q}}{1 + \frac{2\Gamma^*g_c}{\alpha Q}} \frac{K_{sl}|\psi_c|}{1.6Dg_c} \frac{1 + \frac{2\Gamma^*g_c}{\alpha Q}}{1 + \frac{2\Gamma^*g_c}{\alpha Q}}\right).$$

(A7)

In addition to purely using literature values in $LRU_{CAP}$, some of the parameters were also fitted in order to analyze the deficiencies of the model. In particular, two fitting parameters In Eq. (A7) all the parameters are physiologically meaningful

and can be measured independently or obtained from the literature, because the underlying CAP model is based entirely on such parameters. This contrasts with use of the stomatal optimization model of Medlyn et al. (2011), for example, which contains an undetermined parameter ($\lambda$, interpreted as the marginal water cost of carbon gain) that must be empirically fitted.

Nevertheless, to assess the performance of $LRU_{CAP}$ obtained from literature-based parameter values, we compared it with $LRU_{CAP}$ obtained by fitting the two key parameter combinations $X = \frac{|\psi_c|}{1.6g_c}$ and $Y = \frac{2\Gamma^*g_c}{\alpha Q}$ were assigned so that in terms of

which Eq. (A7) became.
A7) may be written as

\[
\text{LRU}_{\text{CAP}} = \frac{1}{1.21} \frac{c_a}{c_a - \Gamma^*} \left(1 + \sqrt{\frac{K_{sl} X}{D} \sqrt{1 + \frac{Y}{Q}}} \right),
\]

(A8)

Parameters X and Y were then optimized to minimize the RMSE of \(\log(\text{LRU}_{\text{CAP}})\) to measured \(\log(\text{LRU})\), due to the logarithmic nature of LRU, with Matlab’s \textit{fminsearch} function. However, we emphasise that this fitting procedure was conducted purely in order to assess the model performance and is not a requirement for applying \(\text{LRU}_{\text{CAP}}\) in practice when literature-based parameter values are available. Moreover, the results presented in this study are not based on the optimized values, but on literature values only.

A2 LRU\textsubscript{CAP} assuming finite mesophyll conductance

In the case that mesophyll conductance is not assumed infinite \(r\) (but boundary layer conductance is \textit{infinite}), Eq. (A1) becomes

\[
\text{LRU} = \frac{1}{1.21} \frac{1}{1 + \frac{g_{\text{CO}_2}^{\text{CO}_2} + g_{\text{CO}_2}^{\text{COS}}}{g_{\text{m}}^{\text{CO}_2} + g_{\text{m}}^{\text{COS}}} \left(1 - \frac{c_i}{c_a}\right)^{-1}}.
\]

(A9)

Further assuming

If we further assume that the ratios of stomatal to mesophyll conductances are the same for \textit{CO}_2 and \textit{COS} and knowing that, then from \(g_{s}^{\text{CO}_2}(c_a - c_i) = g_{m}^{\text{CO}_2}(c_i - c_c)\), where \(c_c\) is the chloroplast \textit{CO}_2 molar mixing ratio (mol mol\(^{-1}\)), we get

\[
\frac{g_{s}^{\text{COS}}}{g_{m}^{\text{COS}}} = \frac{g_{s}^{\text{CO}_2}}{g_{m}^{\text{CO}_2}} = \frac{c_i - c_c}{c_a - c_i}.
\]

(A10)

Implementing in Eq. (A10) into (A9) to obtain

\[
\text{LRU} = \frac{1}{1.21} \left(1 - \frac{c_c}{c_a}\right)^{-1},
\]

(A11)

which reduces to Eq. (A9) gives

\[
\text{LRU} = \frac{1}{1.21} \left(1 - \frac{c_c}{c_a}\right)^{-1}
\]

\[
= \frac{1}{1.21} \frac{c_a}{c_a - \Gamma^*} \left(1 - \frac{c_c}{c_a}\right)^{-1}.
\]

The CAP model predicts the optimal stomatal conductance by maximizing the rate of leaf photosynthesis \(A\) (Dewar et al., 2018) A2) when mesophyll conductance is infinite (since then \(c_c = c_i\)). As noted above, CAP represents NSLs in terms of an apparent downregulation of the \(A - c_i\) response curve (Eq. A3). This empirical observation may be interpreted in various ways: as a downregulation of photosynthetic efficiencies \((\alpha \text{ and } g_a)\) in the chloroplast, or a downregulation of mesophyll conductance.
(\(g_{in}^{CO2}\)), or some combination of the two. In the case that mesophyll conductance is finite and non-stomatal limitations where NSLs act entirely on \(g_{in}^{CO2}\) with no effect on the biochemical efficiencies, \(A\) is given by

\[
A = \frac{\alpha Q g_c(c_c - \Gamma^*)}{\alpha Q + g_c(c_c + \Gamma*)}.
\]

This equation can be used to calculate the value of \(c_c\) as a function of the chloroplast CO\(_2\) concentration by (cf. Eq. A3)

\[
eq c_c - \Gamma^* = \frac{\left(\frac{\alpha Q}{g_c} + 2\Gamma^*\right) A}{\alpha Q - A} \frac{\alpha Q g_c(c_c - \Gamma^*)}{\alpha Q + g_c(c_c + \Gamma^*)}.
\]

(A12)

into which we can then substitute the-

In this case, since Eq. (A3) still holds, we obtain the same optimal CAP solution for stomatal conductance and \(c_c\) (Eq. A4) as before, but now with an additional prediction for the finite (but variable) mesophyll conductance as implied by Eq. (A12), which links the chloroplast CO\(_2\) concentration \((c_c)\) to the CAP solution of \(A\). From Eq. (A12),

\[
c_c - \Gamma^* = \frac{\left(\frac{\alpha Q}{g_c} + 2\Gamma^*\right) A}{\alpha Q - A}.
\]

(A13)

The CAP solution for stomatal conductance is given by Dewar et al. (2018) as (Dewar et al., 2018)

\[
g_s = \frac{\alpha Q}{\frac{\alpha Q}{g_c} + 2\Gamma^*} \frac{x\theta}{x\beta^2 + (1 - x)(x w + 1)}
\]

(A14)

where \(\theta = 1 - \frac{\psi_{soil}}{\psi_c}\)

(A15)

\(w = \frac{c_a - \Gamma^*}{\frac{\alpha Q}{g_c} + 2\Gamma^*}\)

(A16)

\(x = \frac{c_i - \Gamma^*}{c_a - \Gamma^*} = \frac{1}{1 + \beta}\)

(A17)

where in which \(\psi_{soil}\) is the saturated (MPa) is the soil water potential (MPa). Substituting \(x\) as a function of \(\beta\) into Eq. (A14) and simplifying gives

\[
g_s = \frac{\alpha Q}{\frac{\alpha Q}{g_c} + 2\Gamma^*} \frac{\theta}{\beta(1 + \beta + \frac{w}{1 + \beta})}
\]

(A18)
We then find the CAP solution for $A$ as follows:

$$A = g_s(c_a - c_i) = g_s(1 - x) = g_s \frac{\beta}{1 + \beta} = \frac{\alpha Q \hat{c}_a}{g_c + 2 \Gamma^* (1 + \beta)^2 + w}$$

$$A = g_s(c_a - c_i)$$

$$= g_s(c_a - \Gamma^*)(1 - x)$$

$$= g_s(c_a - \Gamma^*) \frac{\beta}{1 + \beta}$$

$$= \frac{\alpha Q (c_a - \Gamma^*)}{g_c + 2 \Gamma^* (1 + \beta)^2 + w} \theta.$$  \hspace{1cm} (A19)

Substituting this into Eq. (A13) and simplifying then gives

$$\hat{c}_c = \frac{\theta}{(1 + \beta)^2 + (1 - \theta) w} = \frac{c_c - \Gamma^*}{(1 + \beta)^2 + (1 - \theta) \frac{2 \Gamma^*}{\alpha Q + 2 \Gamma^* g_c}} = \frac{\theta}{(1 + \beta)^2 + (1 - \theta) \frac{2 \Gamma^*}{\alpha Q + 2 \Gamma^* g_c}}.$$  \hspace{1cm} (A20)

that can finally be substituted into which can be combined with Eq. (A12) for to give the solution of $LRU_{CAP}$ with finite mesophyll conductance.

Similar to As for $LRU_{CAP}$ with infinite mesophyll conductance, this formulation was also fitted in terms of we also fitted this version with respect to parameters $X$ and $Y$. In the parameterization in order to compare with the performance of the model using literature-based values. For this procedure, $\beta$ and $w$ were expressed in terms of $X$ and $Y$ so that

$$\beta = \frac{1}{\sqrt{K_D^X (1 + \frac{Y}{Q})}}$$  \hspace{1cm} (A21)

and

$$w = \frac{c_a - \Gamma^*}{2 \Gamma^* - \frac{Q}{Y} + 1}.$$  \hspace{1cm} (A22)

and implemented then substituted into Eq. (??). However, as for the infinite $g_m$ solution, this fitting procedure was conducted purely in order to assess the model performance and is not a requirement for applying $LRU_{CAP}$ in practice when literature-based parameter values are available.
Figure B1. Modeled against measured NEE using (a) NLR and (b) ANN models for modeling NEE.
Figure B2. Scatter plots of GPP_{\text{air}} that uses only air temperature as the driver for respiration against GPP_{\text{NLR}} that uses an average of air and soil temperatures as the respiration driver in 30 min, daily and monthly time scales. Black line is the least-squares linear fit to the data.
Figure B3. ANOVA test results for 30 min GPP data. Gray bars indicate no difference to the reference (blue) and red bars indicate statistical difference to the reference. The results show that only $\text{GPP}_{\text{COS,PAR}}$ differs statistically from $\text{GPP}_{\text{NLR}}$ on 30 min time scale.
Figure B4. ANOVA test results for daily GPP data. Gray bars indicate no difference to the reference (blue) and red bars indicate statistical difference to the reference. The results show that both GPP\textsubscript{COS,PAR} and GPP\textsubscript{COS,CAP} differ statistically from both GPP\textsubscript{NLR} and GPP\textsubscript{ANN} on daily scale. GPP\textsubscript{COS,PAR} and GPP\textsubscript{COS,CAP} do not differ from each other.
Figure B5. ANOVA test results for monthly GPP data. Gray bars indicate no difference to the reference (blue) and red bars indicate statistical difference to the reference. The results show that all GPPs are statistically the same on monthly scale.
Figure B6. Measured LRU derived from chamber measurements (gray) and modelled LRU_{PAR} (blue) and LRU_{CAP} (red) assuming infinite (a-c) or finite (d-f) mesophyll conductance ($g_m$) in LRU_{CAP} against PAR and VPD. Subplots c and d compare the chamber measured LRU against modelled LRU_{PAR} and LRU_{CAP}.
Figure B7. Net ecosystem exchange (NEE) against photosynthetically active radiation (PAR) close to the compensation point during May, June, July and August. Data are binned to different air temperature classes: $5^\circ \text{C} < T_a < 10^\circ \text{C}$ (blue), $10^\circ \text{C} < T_a < 15^\circ \text{C}$ (orange) and $T_a > 15^\circ \text{C}$ (yellow).
Author contributions. KMK, IM and TV designed the study. KMK, PK and LMJK performed the measurements and flux processing. RD, AM and KMK developed the new LRU formulation. GT provided the GPP estimate by artificial neural networks. All authors contributed by commenting the study design, results and the manuscript. KMK wrote the manuscript with contributions from all co-authors.

Competing interests. The authors declare that they have no conflict of interest.

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