Opinion

The many meanings of gross photosynthesis and their implication for photosynthesis research from leaf to globe

INTRODUCTION

Photosynthesis is a complicated process and its research has a long history (Govindjee & Gest 2002). During this history, components of the photosynthetic process and their interconnections were unravelled only gradually. As the understanding of photosynthesis deepened, terminologies and definitions of key concepts often had to be revised, in many cases, repeatedly, in order to correct earlier mistakes and/or accommodate new findings. For example, the definition of ‘photosynthesis’ itself has been changed many times. American Scientist Charles Barnes (1858–1910) coined the word ‘photosynthesis’, although he preferred to use the word ‘photosyntax’ to describe the light-driven reduction of CO₂ to sugars in plants (Gest 2002). Earlier definitions of photosynthesis included simultaneous reduction of CO₂ and evolution of O₂, only to be corrected later after photosynthetic bacteria were discovered (Blankenship 2002). We are now facing a similar situation with the concept ‘gross photosynthesis’.

‘Gross photosynthesis’ is a term whose use has not been consistent in the long history of photosynthetic research. Historically, plant biochemists and physiologists, who studied photosynthesis at scales less than a leaf, did not consider photorespiration as part of photosynthesis even though photorespiratory CO₂ is released via mitochondria into the cytosol, takes place simultaneously and competitively with CO₂ reduction, and occurs only in light. This is because the discovery of photorespiration was relatively late (Decker 1955) and understanding its fundamental difference from the so-called dark respiration (also known as mitochondrial respiration) took even longer time (Bowes et al. 1971). Once photorespiration was discovered and its mechanism understood, researchers started to use the term ‘true photosynthesis’ to describe the total CO₂ fixation (i.e., a measure of carboxylation or equivalently oxygen evolution in the Hill reaction or all electrons generated by photochemical reactions), not allowing for any loss of CO₂ through dark- and photorespiration. Meanwhile, the term ‘apparent photosynthesis’ was used to describe the difference between true photosynthesis and photorespiration, excluding dark respiration (Hew et al. 1969). Sometime during the following years, the term ‘gross photosynthesis’, which had been used earlier by experimental researchers of aquatic photosynthesis (e.g. Pratt & Berkson 1959), started to appear more frequently in the literature of general plant physiology. In the context of early aquatic studies, gross photosynthesis referred to the difference in oxygen concentrations between the light and dark bottles (Gaarder & Gran 1927; Pratt & Berkson 1959). In hindsight, gross photosynthesis in these early aquatic studies was actually equivalent to apparent photosynthesis because photorespiration occurs in the light bottle, but not in the dark bottle. Despite this early history, gross photosynthesis was used by plant biochemists and physiologists after the discovery of photorespiration to represent true photosynthesis. This use is continued in modern times as can be seen in influential textbooks of terrestrial and aquatic photosynthesis (e.g. Schopfer & Brennike 2010). Accompanying this changed meaning of gross photosynthesis, the term ‘net photosynthesis’ appeared and was used to describe the difference between true (gross) photosynthesis and the total (dark- and photo-) respiratory losses of CO₂, that is, the difference between apparent photosynthesis and dark respiration.

Both gross photosynthesis and net photosynthesis are now key concepts at all scales of photosynthesis research from molecular to leaf to canopy to globe. Unfortunately, the history outlined previously has often been disregarded in the contemporary use of the term ‘gross photosynthesis’ and, to some extent, ‘net photosynthesis’ as well. Consequently, these two terms, particularly gross photosynthesis, have been used inconsistently across space and time scales. This situation is especially serious in ecologically oriented studies of photosynthesis, which have the ultimate goal of quantifying gross primary productivity (GPP). Sometimes, the same researcher may use these two terms for different meanings in the same paper (e.g. Porcar-Castell et al. 2014). The imprecise or incorrect use of different photosynthetic concepts has caused tremendous confusion.

Because of the critical importance of photosynthesis to local, regional and global carbon cycles, it is essential to clear this confusion so that estimates of carbon budgets can be compared across space, time and methods. The present paper attempts to do so. We will appeal for respecting the historical developments of photosynthetic terminologies, which means the following:

- Gross photosynthesis is true photosynthesis (carboxylation).
- Net photosynthesis is true photosynthesis minus photorespiration and dark respiration.
- GPP is intended as an integration of apparent photosynthesis (true photosynthesis minus photorespiration), NOT gross (true) photosynthesis.
We will present rationales behind these appeals and discuss their implications for modelling and measuring photosynthesis at multiple scales. Because the eddy covariance (EC) approach has been playing a foundational role in carbon cycle research (Baldocchi 2008), we will examine the actual meanings of canopy-scale photosynthetic estimates inferred from EC flux measurements.

LEAF-SCALE PHOTOSYNTHESIS TERMINOLOGY

We start with a mathematical description of leaf net photosynthesis \( P_n \) of C\textsubscript{3} plants based on the theory of von Caemmerer & Farquhar (1981):

\[
P_n = V_c - 0.5V_o - R_{day}.
\]  

(1)

Here, \( V_c \) and \( V_o \) represent the rates of carboxylation (true photosynthesis) and oxygenation by the enzyme ribulose bisphosphate carboxygenase/oxygenase (Rubisco), respectively, and \( R_{day} \) represents daytime leaf respiration other than photorespiration. All terms have a unit of moles of CO\textsubscript{2} per unit leaf area and time. 0.5\( V_o \) is photorespiration (often denoted as \( R_{pr} \)). In Eqn 1, we use \( R_{day} \) to differentiate it from leaf dark respiration in the night, \( R_{dark} \) (respiration of a dark-adapted leaf). The relationship between \( R_{day} \) and leaf dark respiration in the night will be discussed later. Here, we employ a sign convention by which component fluxes, such as true photosynthesis (carboxylation rate) and respiration, which do not change sign, are always referred to with a positive sign, while for net fluxes, such as net photosynthesis or the net ecosystem production (NEP), a positive flux represents a net uptake by a leaf or an ecosystem from the atmosphere and a negative flux the reverse. Equation 1 may also be expressed as

\[
P_n = V_c \left( 1 - \frac{R_{pr}}{C_i} \right) - R_{day},
\]  

(2)

where \( R_{pr} \) represents the CO\textsubscript{2} compensation point in the absence of \( R_{day} \) (Pa) and \( C_i \) stands for the CO\textsubscript{2} partial pressure (Pa) inside the intercellular airspace. For convenience, in this formulation, we have ignored, as in most literature of large-scale photosynthesis, the crucial importance of mesophyll diffusion (Sun et al. 2014a,b).

Equations 1 and 2 state that leaf net photosynthesis is the result of the CO\textsubscript{2} carboxylation minus CO\textsubscript{2} losses through photorespiration (for every oxygenation of 1 mol of oxygen, 0.5 mol of CO\textsubscript{2} is released) minus any (mostly) mitochondrial respiration. Both carboxylation and photorespiration occur only in light, whereas mitochondrial respiration continues in dark as well as in light. Equation 2 emphasizes the intrinsic and inseparable link between CO\textsubscript{2} assimilation by carboxylation and release through photorespiration. The ratio \( R_{pr}/C_i \) represents the fraction (up to 50%; Schopfer & Brennike 2010) of carboxylated CO\textsubscript{2} being released through photorespiration. Equations 1 and 2 hold at the scale of single leaves as well as plant canopies, provided appropriate spatial integration is applied (De Pury & Farquhar 1997).

Figure 1 shows the various photosynthesis terms, based on simulations with the Farquhar et al. (1980) model, in a visual fashion.

PHOTOSYNTHETIC TERMS AND THE CENTRAL ROLE OF APPARENT PHOTOSYNTHESIS IN MODELLING AND MEASUREMENTS

Just to emphasize, with respect to the photosynthesis terminology, \( V_c \) corresponds to the term ‘true photosynthesis’, \( V_c - 0.5V_o \) to the term ‘apparent photosynthesis’ (Hew et al. 1969) and \( V_c - 0.5V_o - R_{day} \) to the term ‘net photosynthesis’. Unfortunately, this photosynthetic terminology has not been followed consistently. Both the true photosynthesis and the apparent photosynthesis have been referred to as gross photosynthesis (e.g. Schopfer & Brennike 2010; Porcar-Castell et al. 2014), while net photosynthesis has often been used in place of ‘apparent photosynthesis’. Sometimes, this mixed use of net and apparent photosynthesis is intentional as in full sunlight, the day respiration of a healthy leaf is much smaller than its apparent photosynthesis. But, in other times, researchers may have not realized this term has been misused.

In the carbon cycle research community, a more confusing situation is caused by the use of gross photosynthesis interchangeably with gross primary production/productivity or gross ecosystem production/productivity, abbreviated as GPP or GEP, respectively. Such practice may be prompted by the shared appearance of the word ‘gross’ in these terms. However, this practice conflicts with the historical equivalence of gross photosynthesis with true photosynthesis. It also contradicts with what GPP is intended to be and with the way GPP is actually calculated. For carbon cycle research, knowing true photosynthesis is not as important as knowing...
apparent photosynthesis because photorespiration always accompanies and immediately reduces true photosynthesis. Consequently, it is more meaningful to calculate GPP as the spatial/temporal integration of apparent photosynthesis (i.e., true photosynthesis minus photorespiration), rather than true photosynthesis.

As far as we know, no carbon cycle researchers have calculated or intended to calculate GPP as an integration of true photosynthesis, even though they may use GPP and gross photosynthesis interchangeably. For example, Chapin et al. (2006) defined GPP as ‘the sum of gross carbon fixation by autotrophic carbon-fixing tissues per unit area and time’. But from the context of that paper, it is clear that their gross carbon fixation was meant to be apparent photosynthesis, not true photosynthesis. GPP is also represented in most biogeochemical and land surface models as the difference between carboxylation rate (= true photosynthesis) and photorespiration (e.g., Bonan et al. 2011, Sun et al. 2014a). Interestingly, this calculation of GPP by modern modellers is consistent with the work of early pioneers of canopy photosynthesis research. In their now much celebrated study of canopy dry matter production, Monsi & Saeki (1953) used the following two equations for leaf and canopy, respectively:

\[ A = \frac{bf}{1 + al} - r, \]  
\[ P = \frac{b}{Ka} \ln \left( \frac{1 + aKI_0}{1 + aKI_0 e^{-rF}} \right) - rF. \]  

According to the rather verbatim translation (from German to English) by Marcus Schortememeyer (Monsi & Saeki 2005), these two pioneers called \( A \) leaf net assimilation (equivalent to leaf net photosynthesis \( P_a \) in Eqn 1), \( r \) leaf respiration, and \( P \) canopy productivity \((a \text{ and } b \text{ are empirical constants, } K \text{ extinction coefficient, } F \text{ leaf area index, } I \text{ light intensity inside canopy and } I_0 \text{ light intensity above canopy.)} \)

They called \( bl/(1+al) \) ‘leaf photosynthesis’. By analogy, Monsi and Saeki would have called the corresponding term in the canopy equation (the first term in the left side of Eqn 4) ‘canopy photosynthesis’ (they however did not use this phrase explicitly). Although photorespiration does not appear directly in Monsi and Saeki’s leaf photosynthesis and canopy photosynthesis, it should be considered as an integral part of both terms since \( r \) and \( rF \), which are the only term left when \( I_0 \) and therefore \( I \) are set to zero, clearly denote day respiration at leaf and canopy scales, respectively. Thus, Monsi and Saeki’s leaf photosynthesis and canopy photosynthesis are apparent photosynthesis. The integration of apparent photosynthesis at the canopy scale over time leads to GPP.

True (gross) photosynthesis cannot be directly measured in natural conditions (Larcher 2001), although its approximation may be obtained under low oxygen concentrations (to suppress photorespiration) or by feeding leaves with \(^{12}\text{CO}_2\) and \(^{13}\text{CO}_2\) in sequence and monitoring in- and out-fluxes of these two labelled molecules (Haupt-Herting et al. 2001). Apparent photosynthesis cannot be directly measured either but can be estimated in theory with differential approaches much like the light/dark bottle approach mentioned in the Introduction section. At the leaf scale, this can be achieved by measuring \( \text{CO}_2 \) evolution in the dark and then adding this number to the net photosynthesis obtained in the light to get the apparent photosynthesis (but see the caveats discussed in the next section). The same principle can be and has been applied at the canopy scale. In the early 1900s, researchers already started to use translucent chambers to study the whole-plant \( \text{CO}_2 \) exchange (for a review, see Baldocchi & Amthor 2001). If a translucent chamber is covered with a dark cloth, the dark respiration of the whole plant would be measured. Measurements from the translucent chamber with and without the dark cloth could then be used to calculate the apparent photosynthesis of the whole plant.

Forests are too large to be encased in chambers, but the EC technique (Baldocchi 2008) offers several options, each with its own caveats. One option is to couple an overstory EC system with either an understory EC system or an automated soil chamber system (Baldocchi et al. 1987; Law et al. 1999; Missen et al. 2007). The sum of the net uptake measured by the overstory system and the flux by the understory system equals canopy true photosynthesis minus canopy photosynthesis minus canopy day respiration minus stem respiration. This sum is the counterpart of leaf net photosynthesis (Eq. 1) at the canopy scale and can be properly called canopy net photosynthesis (Baldocchi & Amthor 2001). To obtain canopy apparent photosynthesis, however, one will need estimates of canopy day respiration and stem respiration, as it is the sum of canopy net photosynthesis plus canopy day respiration plus stem respiration.

Stable carbon and oxygen isotopes have been used to partition net ecosystem exchanges of carbon dioxide measured by the EC approach into canopy photosynthesis and ecosystem respiration (Yakir & Wang 1996; Bowling et al. 2001; Griffis 2013). Furthermore, carbonyl sulfide (COS) (Campbell et al. 2008; Wohlfahrt et al. 2012; Berry et al. 2013) and sun-induced chlorophyll fluorescence (Guanter et al. 2014; Parazoo et al. 2014) have been proposed as tracers of canopy photosynthesis. Detailed discussions of these approaches are beyond the scope of this short opinion article. However, we want to point out that it remains to be determined what terms of canopy photosynthesis can be resolved with their application. In the case of stable isotopes, uncertainties associated with fractionations by Rubisco, photorespiration and dark respiration and potentially large differences in isotope compositions among respirations from leaf, stem, root and microbes (e.g. Tcherkez et al. 2011; Ghoshghaie & Badeck 2014) will complicate attempts to partition net fluxes into any components. For the COS approach, uncertain distributions of carbonic anhydrase, the enzyme that catalyses the assimilation of COS, within the mesophyll cell structures (Evans et al. 2009) and in the soil (Wingate et al. 2009) and potential emissions of COS from soil (Maseyk et al. 2014) will challenge COS as a tracer of different canopy photosynthetic components. Chlorophyll fluorescence is a signature of photosynthesis (Papageorgiou & Govindjee 2004). Because chlorophyll fluorescence intensity
induced by sunlight is proportional to the electron transport rate from the photosystem II to photosystem I, which, in turn, is proportional to \( V_c - 0.5V_o \), it should be a measure of apparent photosynthesis. However, the relationship between chlorophyll fluorescence and apparent photosynthesis will be affected by temperature, radiation, water stress and other environmental variables and may not be linear.

Researchers have also exploited the fact that photosynthesis and respiration are driven by different environmental factors to infer the apparent photosynthesis from the EC measurements of the net exchange of CO\(_2\) between the atmosphere and the underlying ecosystem. This has been done in two ways. The first is that during nighttime, the net ecosystem CO\(_2\) exchange consists only of ecosystem respiration (=leaf dark + stem + root + microbial respirations), that is, ‘true photosynthesis’ and photorespiration do not occur (Reichstein et al. 2005). The other is that ecosystem respiration is not a direct function of photosynthetically active radiation (PAR), while both the true photosynthesis and the photorespiration are (Gu et al. 2002). Regardless of which way is exploited, both approaches can only estimate the apparent photosynthesis, not the true photosynthesis. Ironically, due to a potential difference between dark respiration in the night and dark respiration in the day (i.e. day respiration, which occurs in the light), the photosynthetic estimates from EC flux measurements with certain approaches may be closer to the stated but unintended gross (true) photosynthesis than to the unstated but intended apparent photosynthesis. This issue is addressed next.

**IMPLICATIONS FOR EC CO\(_2\) FLUX PARTITIONING**

EC CO\(_2\) flux measurements above active vegetation are characterized by fluxes of generally opposing sign during day and night. During nighttime, in the absence of photosynthetically active radiation, the nighttime net ecosystem production (NEP\(_n\)) reflects only CO\(_2\) release to the atmosphere, that is,

\[
\text{NEP}_n = -(R_{\text{dark}} + R_{\text{non-leaf}})
\]

where \( R_{\text{dark}} \) represents leaf respiration during darkness and \( R_{\text{non-leaf}} \) collectively summarizes respiration from all other plant organs (e.g. wood, root) and heterotrophic organisms (microorganisms, animals). Here, we use the term NEP synonymously to net ecosystem CO\(_2\) exchange (NEE) and refer to Chapin et al. (2006) for a thorough discussion of the practical differences between the two terms, which are however neglected in the context of the present paper.

At the same temperature, \( R_{\text{dark}} \) is typically larger than \( R_{\text{day}} \) (0.2 < \( R_{\text{day}}/R_{\text{dark}} \) < 1.3) (Heskel et al. 2013; Niinemets 2014) due to mitochondrial respiration being suppressed in the presence of light (Atkin et al. 1997) and/or because part of the CO\(_2\) produced by mitochondrial respiration is re-fixed by photosynthesis (Pinelli & Loreto 2003). The degree to which \( R_{\text{day}}/R_{\text{dark}} \) < 1 is however highly uncertain due to challenges in reliably estimating \( R_{\text{day}} \) (Gu & Sun 2014). In any case, due to the absence of radiation and thus photosynthesis, NEP\(_n\) has no contribution from photorespiration.

During daytime, \( R_{\text{day}} < R_{\text{dark}} \) (but see above) and NEP\(_n\) in addition to \( R_{\text{non-leaf}} \), includes CO\(_2\) uptake by carboxylation and CO\(_2\) loss by photorespiration, that is,

\[
\text{NEP}_n = V_c - 0.5V_o - (R_{\text{day}} + R_{\text{non-leaf}})
\]

The partitioning algorithms (Falge et al. 2001; Reichstein et al. 2005; Lasslop et al. 2010b) that are presently used within the FLUXNET project (Baldocchi 2008) intend to solve Eqn 6 for the ‘apparent’ (\( V_c - 0.5V_o \)) photosynthesis (even though they may state to estimate gross photosynthesis), which requires estimating \( R_{\text{day}} + R_{\text{non-leaf}} \). To achieve so, the FLUXNET algorithms extrapolate the respiration terms in Eqn 5, which are collectively referred to as ecosystem respiration (\( R_{\text{eco}} \)), to daytime conditions by parameterizing \( R_{\text{eco}} \) as a function of temperature (Reichstein et al. 2005; Lasslop et al. 2010b).

Because \( R_{\text{dark}} \) is typically even though the actual degree is highly uncertain (Gu & Sun 2014), larger than \( R_{\text{day}} \), extrapolation of nighttime measurements to daytime conditions overestimates \( R_{\text{day}} \) and consequently the ‘apparent photosynthesis’. This issue has been known in the EC CO\(_2\) flux community for over a decade (e.g. Janssens et al. 2001) and Wohlfart et al. (2005) have shown this overestimation to amount to ca. 11–17%.

Because NEP\(_n\) overestimates \( R_{\text{day}} \) and does not include \( R_{\text{gr}} \), the FLUXNET estimate of apparent photosynthesis (GPP) may be quantitatively closer to the stated but unintended ‘true’ than the unstated but intended ‘apparent’ photosynthesis. To explore this possibility, we have used the sun/shade big-leaf model by De Pury & Farquhar (1997), which consists of the Farquhar et al. (1980) model of leaf net photosynthesis integrated with a big-leaf canopy radiative transfer model which distinguishes between sunlit and shaded leaf area fractions. The reduction of \( R_{\text{day}} \) compared with \( R_{\text{dark}} \) was included into the model of leaf net photosynthesis based on Wohlfart et al. (2005). Simulations were conducted by varying incident photosynthetically active radiation to generate light response curves of canopy scale \( V_c \), \( V_c - 0.5V_o \), and \( R_{\text{day}} \) (\( R_{\text{dark}} \) at zero light). The leaf area index (2 m\(^2\) m\(^{-2}\)), temperature (25 °C), intercellular CO\(_2\) and O\(_2\) partial pressures (25 Pa and 21 kPa), the fraction of diffuse radiation (0.1) and the sun’s angle (65°) were kept constant to this end. \( R_{\text{non-leaf}} \) was parameterized as a fixed fraction (0.4) of \( R_{\text{dark}} \) for the sake of simplicity and the NEP\(_n\) and NEP\(_p\) were calculated according to Eqs 3 and 4, respectively. The FLUXNET partitioning approach was then mimicked by subtracting nighttime \( R_{\text{eco}} \) that is, \( R_{\text{day}} + R_{\text{non-leaf}} \) (Eqn 5), from the calculated NEP\(_p\). As shown in Fig. 2, \( R_{\text{eco}} \) determined with the flux partitioning approach exceeded the true \( R_{\text{eco}} \) at low light levels because \( R_{\text{day}} \) was overestimated. The overestimation was larger than the value of \( R_{\text{gr}} \), which was relatively small at low light conditions. As a consequence, the estimated ‘apparent photosynthesis’ exceeded not only the correct ‘apparent photosynthesis’ (\( V_c - 0.5V_o \)) but also the ‘true photosynthesis’ (\( V_c \)). As the intensity of incident radiation increased, \( R_{\text{gr}} \)
increased with the rising carboxylation rate and $R_{\text{day}}$ decreased due to the progressive inhibition of $R_{\text{dark}}$ and eventually $R_{\text{eco}}$ estimated with the flux partitioning approach fell short of the true $R_{\text{eco}}$ and the inferred ‘apparent photosynthesis’ settled between the correct ‘apparent’ and ‘true’ photosynthesis. Overall, the ‘apparent photosynthesis’ estimated with the flux partitioning approach produced estimates that were closer to the ‘true photosynthesis’ than the correct ‘apparent photosynthesis’.

The overestimation at low and the underestimation at high levels of incident radiation shown in Fig. 2 suggests that the ‘apparent photosynthesis’ estimated with the flux partitioning approach may converge to the ‘true photosynthesis’ over the daily cycle. In order to explore this issue, the model as described earlier was forced with seasonally varying measurements of environmental drivers (air and soil temperature, direct and diffuse photosynthetically active radiation) and leaf area index of a temperate mountain grassland based on the dataset used already by Wohlfahrt et al. (2005) for exploring the consequences of the reduction $R_{\text{day}}$ compared to $R_{\text{dark}}$ on the inferred apparent photosynthesis (GPP). $R_{\text{non-leaf}}$ was replaced with simulations of soil respiration as detailed in Wohlfahrt et al. (2005); otherwise, the same procedure as described earlier was followed. As shown in Fig. 3a, the daily average ‘apparent photosynthesis’ as determined with the flux partitioning approach overestimated the ‘true photosynthesis’ by only 3% (Fig. 3a; Wohlfahrt et al. 2005). Seasonal variations of the leaf area index turned out to be a major driver of the discrepancy between both approaches as the underestimation of the inferred ‘apparent photosynthesis’ with respect to the ‘true photosynthesis’ switched to overestimation at leaf area indices around 3 m$^2$ m$^{-2}$ (Fig. 3b). As noted already by Wohlfahrt et al. (2005), these simulations are highly sensitive to the degree of reduction of $R_{\text{day}}$ with respect to $R_{\text{dark}}$ and in addition to the ratio between $R_{\text{dark}}$ and the maximum carboxylation efficiency (Heskel et al. 2013; Niinemets 2014). Understanding of both processes is presently, in particular compared to photosynthesis, insufficient and thus their relative importance poorly constrained (Niinemets 2014). The sensitivity of the simulations to the ratio of $R_{\text{day}}/R_{\text{dark}}$ is exemplified in Fig. 3c, which shows how the ratio between the inferred ‘apparent photosynthesis’ and the ‘true photosynthesis’ changes as a function of $R_{\text{day}}/R_{\text{dark}}$. In our case study, a 10% in the $R_{\text{day}}/R_{\text{dark}}$ translated into a change in the ratio between the inferred ‘apparent photosynthesis’ and the ‘true photosynthesis’ of ca. 3% (Fig. 3c).

**CONCLUSIONS**

We have reviewed the background of leaf photosynthesis and the associated terminology and showed that two differing definitions of gross photosynthesis are used in the literature. The first definition equates gross photosynthesis with the carboxylation rate, which historically has been referred to as ‘true photosynthesis’, while the second definition subsumes carboxylation with photorespiration, which historically has been referred to as ‘apparent photosynthesis’.

We further show that the commonly applied EC CO$_2$ flux partitioning (Reichstein et al. 2005; Lasslop et al. 2010b) yields estimates of GPP which conceptually correspond to the definition of the ‘apparent photosynthesis’ due to the fact that the nighttime ecosystem respiration on which estimated daytime ecosystem respiration is based does not contain any information on photorespiration. The major new finding of this study is that despite being conceptually not compatible with the definition of ‘true photosynthesis’, GPP inferred by flux partitioning is quantitatively actually closer to the ‘true’ than the ‘apparent’ photosynthesis. This is due to an overestimation of daytime mitochondrial respiration with the flux partitioning approach. The actual degree of overestimation is shown to be the result of a complex interplay between biotic and abiotic influence factors and thus varies seasonally (Fig. 3b) and, although not tested here, very much likely between study sites. While GPP estimated with the flux partitioning approach was still somewhat overestimated in the investigated mountain grassland over the annual cycle, underestimation occurred during certain times as well (Fig. 3b) and might dominate under certain conditions.

A key uncertainty (Fig. 3c), and at the same time highly sensitive parameter (Wohlfahrt et al. 2005), is the actual degree to which leaf mitochondrial respiration is reduced in the light relative to darkness, which according to Niinemets (2014) and Heskel et al. (2013) varies between 20 and 130%. Due to technical challenges in reliably estimating $R_{\text{day}}$, available $R_{\text{day}}/R_{\text{dark}}$ ratios should be viewed with caution and it is presently not clear whether this large degree of variation is reflective of biological variability or experimental artefacts. In addition, Pinelli & Loreto (2003) suggested that the
reduction of \( R_{\text{day}} \) in the light might actually be an apparent one, the \( \text{CO}_2 \) released by mitochondrial respiration being re-fixed by photosynthesis. In the latter case or more generally if \( R_{\text{day}}/R_{\text{dark}} \approx 1 \), the flux partitioning approach would result in unbiased estimates of the ‘apparent photosynthesis’ (\( V_c - 0.5V_o \)) and would underestimate the ‘true photosynthesis’ (\( V_c \)) by the flux of photorespiration.

Finally, a word of caution is in order: The present study exclusively focused on issues of photosynthesis terminology in context with the approach of EC flux partitioning and did not quantify other uncertainties with this approach. The uncertainty of nighttime EC \( \text{CO}_2 \) flux measurements is one of these issues (Aubinet 2008). Another one is that the extrapolation of nighttime \( \text{CO}_2 \) flux measurements based on a simple temperature-dependent model to daytime conditions ignores other drivers of diurnal variations in respiration rates, as it has been shown that temperature-independent biotic and abiotic processes play a major role in modulating diurnal variations in ecosystem respiration components (e.g. Bahn et al. 2009; Vargas et al. 2011). Other authors (Vickers et al. 2009) have criticized that flux partitioning creates a spurious correlation between nighttime ecosystem respiration and apparent photosynthesis (but see reply by Lasslop et al. 2010a). Given the complexity of the processes involved and the associated theoretical and experimental uncertainties, it may be worthwhile to question how meaningful EC \( \text{CO}_2 \) flux partitioning is and to seek other ways of exploiting the strong contrast between night and daytime net ecosystem \( \text{CO}_2 \) exchange.

These measurement and methodological uncertainties call for strict use of photosynthetic terminologies so that communications among researchers and across disciplines can be facilitated. For all the purposes of what gross primary production (GPP) has been used for, this GPP has been and has to continue to be calculated as an integration of ‘apparent

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**Figure 3.** (a) Comparison between the ‘true photosynthesis’ (\( V_c \)) and the ‘apparent photosynthesis’ inferred by means of the flux partitioning approach accounting only for the overestimation of leaf day respiration (\( R_{\text{day}} \); red symbols) and in addition for the underestimation of photorespiration (\( R_{\text{pr}} \); blue symbols). Solid lines represent linear regressions forced through the origin with slopes of 1.03 (blue line) and 1.13 (red line). (b) Ratio of inferred ‘apparent’ to ‘true’ photosynthesis (accounting for both the overestimation of leaf day respiration and the underestimation of photorespiration) as a function of the leaf area index as it varies during the course of the season.

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photosynthesis’ as knowing true photosynthesis without simultaneously knowing photorespiration is practically useless. Meanwhile, the carbon cycle research community should pay attention to the misuse of the concepts of gross photosynthesis and to some extent, net photosynthesis and stick to the historical use of these terms as outlined in the end of the Introduction section. To avoid confusion with GPP, we suggest that true photosynthesis is used in place of gross photosynthesis.

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