


## Review Article

# Emerging approaches to measure photosynthesis from the leaf to the ecosystem

Matthew H. Siebers<sup>1,2,3,\*</sup>, Nuria Gomez-Casanovas<sup>2,3,\*</sup>, Peng Fu<sup>2,3</sup>, Katherine Meacham-Hensold<sup>2,3</sup>, Caitlin E. Moore<sup>4,5,6</sup> and  Carl J. Bernacchi<sup>1,2,3,4,5</sup>

<sup>1</sup>United States Department of Agriculture, Global Change and Photosynthesis Research Unit, Agricultural Research Service, Urbana, IL 61801, U.S.A.; <sup>2</sup>Carl R. Woese Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, U.S.A.; <sup>3</sup>Departments of Plant Biology and Crop Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61801, U.S.A.; <sup>4</sup>Center for Advanced Bioenergy and Bioproducts Innovation, University of Illinois at Urbana-Champaign, Urbana, IL 61801, U.S.A.; <sup>5</sup>Institute for Sustainability, Energy & Environment, University of Illinois at Urbana-Champaign, Urbana, IL 61801, U.S.A.; <sup>6</sup>School of Agriculture and Environment, The University of Western Australia, Crawley, WA 6009, Australia

**Correspondence:** Carl Bernacchi (carl.bernacchi@usda.gov)



Measuring photosynthesis is critical for quantifying and modeling leaf to regional scale productivity of managed and natural ecosystems. This review explores existing and novel advances in photosynthesis measurements that are certain to provide innovative directions in plant science research. First, we address gas exchange approaches from leaf to ecosystem scales. Leaf level gas exchange is a mature method but recent improvements to the user interface and environmental controls of commercial systems have resulted in faster and higher quality data collection. Canopy chamber and micrometeorological methods have also become more standardized tools and have an advanced understanding of ecosystem functioning under a changing environment and through long time series data coupled with community data sharing. Second, we review proximal and remote sensing approaches to measure photosynthesis, including hyperspectral reflectance- and fluorescence-based techniques. These techniques have long been used with aircraft and orbiting satellites, but lower-cost sensors and improved statistical analyses are allowing these techniques to become applicable at smaller scales to quantify changes in the underlying biochemistry of photosynthesis. Within the past decade measurements of chlorophyll fluorescence from earth-orbiting satellites have measured Solar Induced Fluorescence (SIF) enabling estimates of global ecosystem productivity. Finally, we highlight that stronger interactions of scientists across disciplines will benefit our capacity to accurately estimate productivity at regional and global scales. Applying the multiple techniques outlined in this review at scales from the leaf to the globe are likely to advance understanding of plant functioning from the organelle to the ecosystem.

## Introduction

The terrestrial biosphere consists of an assemblage of diverse ecosystems. Its complexity is illustrated with a diversity of plants with distinct canopy structures subject to changing environmental conditions. Life on earth relies on the energy captured by these ecosystems through photosynthesis, which accounts for the single largest flux associated with the global carbon cycle [1]. Photosynthesis varies among plant functional types (e.g. C3 vs. C4) and over a wide range of spatial and temporal scales associated with changes in light, temperature, water and nutrients [2,3]. Global climate change driven by anthropogenic activities is having profound impacts on terrestrial ecosystems, with global temperatures rising faster than worst-case predictions [4]. Increasing agricultural demands associated with a growing population requires a doubling of crop yields by 2050 to keep up with demands [5], yet current rates of improvement fall short of this goal [6,7], which is likely to suffer with continued global warming [8–11].

\*Authors request that M.H. Siebers and N. Gomez-Casanovas be considered co-first authors.

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Photosynthesis is a highly complex and relatively inefficient process, yet it is a critical component of the biosphere. Understanding photosynthetic responses over a range of spatial and temporal scales is needed to understand current and to predict future global carbon cycling. This understanding will also lead to improving photosynthesis, which can lead to higher productivity to meet growing agricultural demands [12,13]. These goals can only be achieved through the ability to measure photosynthesis over time and space, yet photosynthesis is difficult to measure directly. This is due to the multiple processes that are represented by the exchange of CO<sub>2</sub> between plants/ecosystems and the surrounding air. For example, at the leaf scale CO<sub>2</sub> is removed from the air by photosynthesis but this is partially countered by photorespiration and respiration, both of which release CO<sub>2</sub> [14,15]. The combined fluxes of these three processes represents net carbon assimilation (*A*) and partitioning this net flux into the component fluxes is challenging [16]. Scaling beyond the leaf only presents additional challenges. At canopy or ecosystem scales, respiration from non-photosynthetic tissues and heterotrophic organisms also release CO<sub>2</sub>, which combined with *A* provide measures of Net Ecosystem Exchange (NEE; Table 1). In this review, we outline the current and emerging approaches to measure photosynthesis at multiple scales and address the challenges and opportunities at each scale (Figure 1). We begin with a focus on the well-established and widely used gas exchange techniques and follow with more recent approaches made available through recent technological advances.

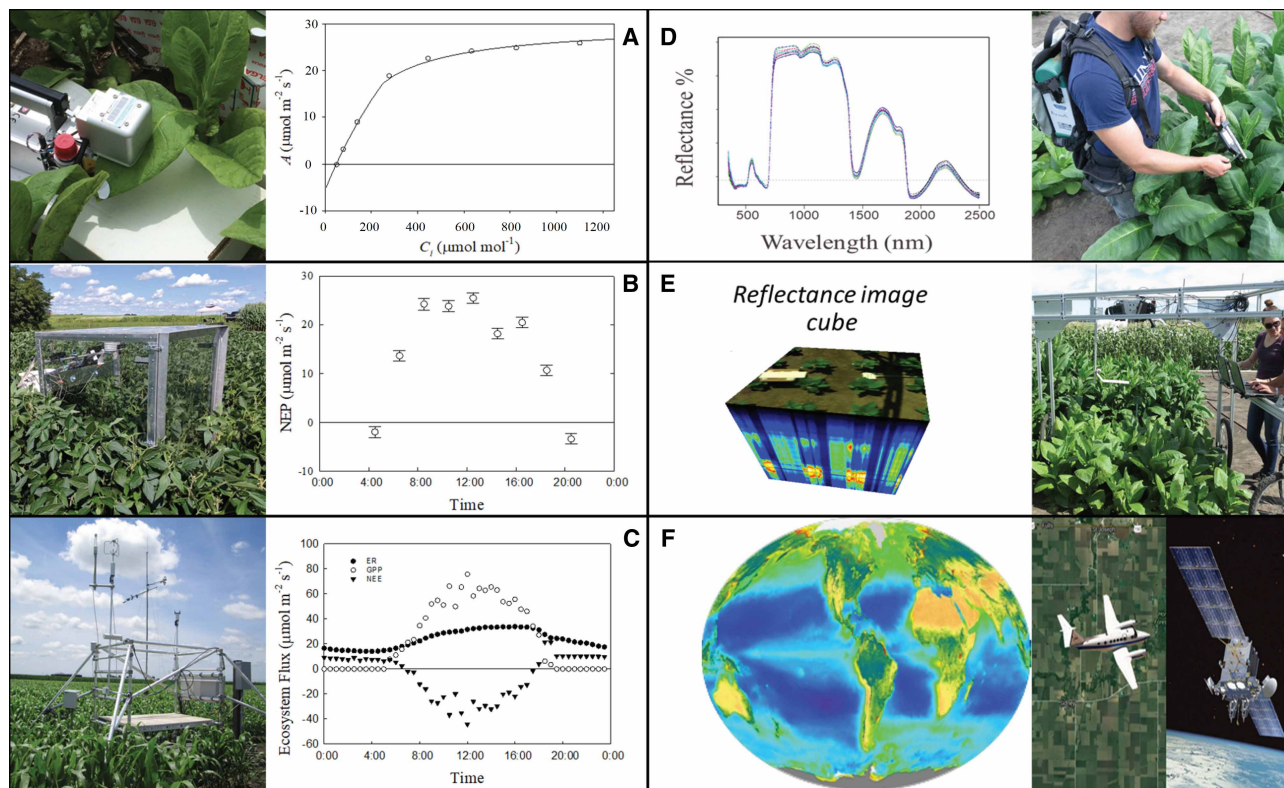
## Gas exchange

The fundamentals of gas exchange at any scale are relatively similar and require the ability to measure gas concentrations in air surrounding and the flow rate in which the air interacts with photosynthetic tissue. In addition to these measurements, numerous assumptions, corrections, and parameterizations are required to fully exploit the power of this technique [16,17]. Gas exchange methods have been applied at scales ranging from the organelle (e.g. [18,19]) to the whole ecosystem/region [20] to provide a basic understanding of how leaves, plants, and ecosystems function and respond to their environment (Figure 1). Historically, gas exchange measurements were limited to enclosed sampling chambers, ranging from sections of leaves to whole plant canopies, where the rate of CO<sub>2</sub> exchange was measured over time. With the advent of micrometeorological techniques, gas exchange measurements at large scales (e.g. whole ecosystems) were developed that removed the need for enclosures (Table 2). Despite errors, uncertainties and challenges associated with gas exchange, the various techniques are the current ‘gold standard’ by which emerging techniques are compared. This section provides an overview of gas exchange measurements at the leaf to ecosystem scales as a baseline in the understanding of emerging techniques.

**Table 1 Terminology associated with photosynthesis at both the leaf and ecosystem levels**

Term	Definition
Gross photosynthesis	The total CO <sub>2</sub> fixed through carboxylation within the leaf chloroplasts.
Apparent photosynthesis	CO <sub>2</sub> assimilated through carboxylation minus photorespiration, a process that involves the oxygenation of Rubisco. The term apparent photosynthesis excludes respiration.
Net Carbon Assimilation ( <i>A</i> )	Gross photosynthesis, minus photorespiration and respiration
Gross Primary Productivity (GPP)	Ecosystem and canopy scale apparent photosynthesis.
Net Primary Productivity (NPP)	Ecosystem and canopy scale apparent photosynthesis minus plant respiration, which includes the CO <sub>2</sub> emitted by both above- and root components (autotrophic respiration, <i>R<sub>a</sub></i> ). NPP is defined with the following equation: $NPP = GPP - R_a$
Net Ecosystem CO <sub>2</sub> Exchange (NEE)	Ecosystem net exchange of CO <sub>2</sub> between an ecosystem and the atmosphere over a given time which can be from hours to years. NEE can be measured using the eddy covariance (EC) as well as biometric methods. The eddy covariance method measures continuous NEE fluxes over time and it is the net balance between GPP and ecosystem respiration ( <i>R<sub>eco</sub></i> ). <i>R<sub>eco</sub></i> is the sum of <i>R<sub>a</sub></i> and soil microbial respiration in aerobic conditions (heterotrophic respiration, <i>R<sub>h</sub></i> ). Biometric methods estimate NEE according to the following equation: $NEE = NPP - R_h$ [116]

In general, photosynthesis is defined as the process by which plants capture light energy and atmospheric CO<sub>2</sub> to synthesize complex carbohydrates. Photosynthesis supports the production of food, fiber, wood, grain fed to livestock, and fuel for humanity and regulates the concentration of CO<sub>2</sub> in the atmosphere. Quantifying global terrestrial photosynthesis is essential to understanding the global CO<sub>2</sub> cycle in a changing environment and the climate system.



**Figure 1.** Depiction of techniques and example data for gas exchange (A–C) and proximal/remote sensing (D–F) techniques used to measure photosynthesis.

(A) Leaf-level gas exchange with one measured representative photosynthetic  $\text{CO}_2$  response curve. (B) Canopy photosynthesis chamber situated over a soybean field with representative diurnal Net Ecosystem Productivity (NEP) data (Image Credit: Anthony DiGrado). (C) Ecosystem-scale eddy covariance system situated over sorghum with representative Net Ecosystem Exchange (NEE; negative values signify downward flux from atmosphere toward land surface) partitioned into Gross Primary Productivity (GPP) and Ecosystem Respiration (ER). (D) leaf hyperspectral point sensor being used on the model crop tobacco and representative spectral reflectance measurements. (E) A hyperspectral imaging sensor measuring plots of the model crop tobacco and an example hypercube showing the visible surface and spectral information for each pixel with depth of image. (F) aircraft and satellite depicted over the earth surface and a map of GPP (public domain image courtesy of GeoEye/NASA SeaWiFS project). Other than where indicated, all images were taken by authors.

## Leaf scale gas exchange

Knowledge of leaf photosynthetic physiology stems from the development and application of leaf-level gas exchange systems [16]. Gas exchange technology has matured to the point where commercial gas exchange systems are widely available from many vendors. In addition to providing the key variables necessary to assess leaf scale carbon assimilation, these systems now provide the opportunity to precisely control the environmental conditions surrounding the photosynthetic tissue and to measure more than just carbon assimilation, including but not limited to transpiration, intercellular  $\text{CO}_2$  concentrations, and stomatal conductance. Gas exchange techniques have been used for decades and most recent advancements have focused on improvements in accuracy, precision, usability, environmental control, and reduction in time to stable measurements. Despite the ease with which leaf level gas exchange can be measured, the importance of understanding gas exchange theory to ensure proper measurement and analysis cannot be overstated.

Gas exchange systems are the most commonly utilized technique for leaf scale photosynthetic measurements. While systems provide measures of  $A$ , various techniques can be applied to separate fluxes of photosynthesis, photorespiration, and respiration. However, many challenges exist with gas exchange that limit the wide application of the technique. These include cost, usability, data processing requirements, and time needed for ensuring quality measurements. Off-the-shelf gas exchange systems cost tens of thousands of dollars and require

**Table 2 Advantages and disadvantages of the canopy and eddy covariance methods to measure CO<sub>2</sub> fluxes and estimate GPP at the ecosystem scale**

	<b>Eddy covariance method</b>	<b>Automated chamber methods</b>	<b>Manual chamber methods</b>
Ecosystem	Short and tall vegetation	Short and tall vegetation	Short and tall vegetation
Temporal sampling frequency	Continuous real-time measurements CO <sub>2</sub> data as well as other data crucial to compute fluxes are obtained at high frequency (at or above 10 Hz)	Continuous measurements	Measurements often made at weekly to monthly intervals for the growing season or an entire year, and over a specific period of the day believed to be representative of the daily CO <sub>2</sub> flux.
Spatial integration	Integrates large spatial areas, called the flux footprint, between hundred meters to several kilometers	Several meters per chamber Scale up necessary	Hundred meters as they are portable Scale up necessary
Accuracy	Most accurate when the atmospheric conditions (wind, temperature, humidity, CO <sub>2</sub> ) are favorable, vegetation is homogeneous and sensors are installed on flat terrain for an extended distance upwind.	Soil and vegetation disturbance possible Significant alteration of canopy microclimate from enclosure	Soil and vegetation disturbance possible Significant alteration of canopy microclimate from enclosure
Gap filling to obtain annual CO <sub>2</sub> fluxes	Gap filling necessary due to the malfunctioning of sensors, power failures, harsh environmental conditions, sensor calibration, lack of turbulence, when wind is coming from an undesirable direction.	Gap filling necessary due to the malfunctioning sensors, power failures, harsh environmental conditions, sensor calibration, lack of turbulence, when wind is coming from an undesirable direction.	Gap filling necessary as measurements are not continuous
Logistical effort	Considerable, especially in remote sites and in hostile environments.	Considerable, especially if appropriate spatial replication is desirable	High personnel effort especially if several instruments are deployed at once to minimize confounding effects resulting from hourly variability
Cost	High due to the cost of fast response instruments	High due to the number of instruments needed for appropriate spatial replication	Lower costs but require more person-hours to collect data

The global eddy covariance network, called FLUXNET (<https://fluxnet.org/about/>), includes measurement sites linked across regional networks in North, Central and South America, Europe, Asia, Africa, and Australia.

frequent maintenance that challenges their widespread use. Most gas exchange systems limit the area of measurement to, at most, several cm<sup>2</sup>, which presents issues related to scaling photosynthesis beyond a small section of one leaf. Typical measurements of *in situ* gas exchange require a minimum of 2–3 min to allow for both the system and the leaf to stabilize. Using these systems to measure beyond a simple survey of gas exchange, for example to measure light response or CO<sub>2</sub> response curves of *A*, requires substantially more time for each leaf. Recent techniques that exploit improved instrument precision can reduce the time for some measurements but generally at the expense of accuracy, and often require more advanced post-processing [21].

### Canopy and ecosystem scale gas exchange

Scaling gas exchange measurements to the canopy or whole ecosystem presents significantly more challenges than at the leaf level, yet there are also more options (Table 2). Canopy chambers work in much the same way as leaf chambers, although at a larger scale. The general principle follows that of leaf-level measurements, although chambers are required to be much larger to encompass multiple plants and the potential is greater for errors associated with leaks or pressure fluctuations [17]. Canopy chambers have been extensively used to measure CO<sub>2</sub> fluxes for a wide range of vegetation types and their strengths lie in their ability to address small-scale spatial variability (Table 2). Furthermore, canopy chambers have been used both as a measurement and treatment system in global change studies to impose treatments as open-top chambers and acting as sample chambers when enclosed (e.g. [22]). Canopy chambers, however, can be limited in sampling frequency and spatial integration (Table 2) while also having a profound impact on the canopy microclimate.

Micrometeorological approaches to gas exchange lack the need for chambers but require large spatial areas (>4 Ha) and a sensor suite that can measure the upward/downward movement of air coupled with the gas concentrations in the air [20]. The dominant micrometeorological technique, eddy covariance (EC), provides near-continuous measurements of NEE integrated over large spatial areas, called the flux footprint, with minimal disturbance (Table 2) [20]. Air flow over a canopy consists of numerous rotating eddies. Measuring the speed and CO<sub>2</sub> concentrations of the eddies moving air upward and downward, provides the basic data needed to calculate fluxes of the footprint, which varies with wind speed and direction [23]. EC requires several important considerations to ensure the NEE data are robust and reliable [24], including ensuring sufficient atmospheric turbulence [23], applying corrections to exclude data fluxes extending beyond the area of measurements [25,26], and ensuring all measured fluxes follow the laws of thermodynamics [27,28] (Table 3). Because of inevitable gaps in data collection associated with field instrumentation, gap filling strategies are used to complete the time-series of flux data (Table 4). In addition to NEE, EC can apply to any measurable component of the atmosphere provided high temporal resolution sensors ( $\geq 10$  Hz) exist (e.g. water vapor, methane, etc.). A global EC flux network, called FLUXNET, provides data from over 900 sites globally, allowing for a link between ecosystem and global NEE. This network provides unprecedented insights into environmental and biological drivers of ecosystem NEE [3,20,29–33]. Among other purposes, the long-term measurements of NEE from this network have improved understanding of ecosystem responses to climate and land-use change [34], and the data are essential to validate remote sensing and modeling products that scale to regions and the globe [35,36].

Whether using chamber-based or micrometeorological approaches, measured NEE provides an opportunity to explore changes in ecosystem-scale gas exchange at high temporal frequency. Photosynthesis at the ecosystem scale is generally defined as gross primary productivity (GPP), which is only one component of NEE. GPP is derived as the difference between measured NEE and modeled ecosystem respiration (ER; Table 5). Obtaining GPP from NEE involves modeling ER using temperature and light response functions; a process typically referred to as flux partitioning [24,32,37,38]. Flux partitioning allows for the investigation over time of GPP

**Table 3 Challenges for obtaining robust estimates of net ecosystem exchange (NEE), and thus gross primary productivity (GPP), from eddy covariance (EC) flux towers used for assessing ecosystem-scale photosynthesis, and description of how scientists working in the field of micrometeorology address these challenges to reduce uncertainty in NEE measurements and GPP estimates [24]**

The obstacle	The cause	The remedy
Missing raw data	Power failure, instrument malfunction, communication issues	Gap fill meteorological variables and use these as divers to build a complete NEE timeseries [41,117]
Atmospheric turbulence	Periods of low atmospheric turbulence reduce the dominance of vertical turbulent transfer, thus violating the assumptions of eddy covariance theory.	Calculate a turbulence threshold ( $u^*$ ) and apply it to flux data to exclude data below the $u^*$ limit -Moving Point Threshold (MPT) -Change Point Detection (CPD) [23,118]
Footprint filters	The measurement area of the flux instruments changes with turbulence. As atmospheric conditions become stable, the area the flux instruments sample from becomes larger. This can extend beyond the ecosystem of interest and bias flux measurements	Apply a footprint exclusion filter [25,26]
Canopy storage	If turbulent mixing is reduced, fluxes can build up within the canopy of interest and result in underestimation of fluxes	Install a profile system to quantify at multiple depths through the canopy [119]
Gap filling uncertainty	Uncertainty in the fluxes due to random errors occurring during measurement and modeling errors during gap filling	Calculate random and model error to provide an estimate of flux uncertainty [120,121]
Partitioning methods	Uncertainty arising due to the flux partitioning model used to estimate GPP	Partition with multiple methods and provide model fit statistics with GPP estimate [117]
Energy balance closure	Based on surface energy balance theory. Net radiation (Rn) minus ground heat flux (G) should be equal to the sum of sensible (H) and latent (LE) heat flux. When this is not the case, there is greater uncertainty in the fluxes.	Calculate the linear regression to obtain the difference between available energy (Rn-G) and energy used in the fluxes (H + LE). The energy used in fluxes is often corrected using the slope of this linear relationship. [27,28]

Some of these challenges include ensuring sufficient atmospheric turbulent conditions are met [23], applying footprint corrections to exclude data when a significant portion of fluxes occur outside the ecosystem region of interest [25,26], and quantifying energy balance closure at the site [27,28]. Improving the robustness of NEE estimates from flux towers is an area of active research in the flux community, and one which will lead to greater understanding of ecosystem photosynthesis across a diversity of biomes.

**Table 4 Description of common methods to fill missing half-hour values in CO<sub>2</sub> records and performance to obtain accurate annual CO<sub>2</sub> sums (i.e. sum of half-hour CO<sub>2</sub> fluxes over a year)**

Gap filling method	Description	Reliability of annual sum of the net CO <sub>2</sub> exchange
Mean Diurnal Variation (MDV) [122,123]	Half-hour CO <sub>2</sub> gaps are replaced by the mean for that half-hour time period based on adjacent days.	Good
Look-up Tables (LUT) [122,123]	Half-hour CO <sub>2</sub> gaps are filled using tables created for each site based on the environmental variables associated with the missing data. These meteorological variables are gross radiation, air temperature and vapor pressure deficit, which are known to regulate CO <sub>2</sub> fluxes. Gaps are filled with available CO <sub>2</sub> data when this set of environmental variables are similar for the missing half-hour CO <sub>2</sub> flux and the available CO <sub>2</sub> data	Good
Marginal Distribution Sampling (MDS) [122,123]	Half-hour CO <sub>2</sub> gaps are filled by a half-hour CO <sub>2</sub> values with similar meteorological conditions in the temporal vicinity of the gap to be filled. This method is a moving LUT technique that exploits the temporal auto-correlation structure of CO <sub>2</sub> fluxes.	Good
Combination of MDS and MDV [124]	When meteorological variables regulating CO <sub>2</sub> fluxes are available, the half-hour CO <sub>2</sub> gap is filled using the MDS method with a moveable time window. When meteorological variables are not available, the missing value is filled using the MDV method with a short window size (i.e. the same day) and the window size can increase until the value can be filled.	Good
Non-linear regressions [122,123]	Half-hour CO <sub>2</sub> gaps are filled using the relationships between available CO <sub>2</sub> fluxes and associated controlling environmental factors during the period of missing fluxes.	Good performance in general, although outliers can contribute to a high bias in predicted fluxes
Artificial Neural networks [123]	Half-hour CO <sub>2</sub> gaps are filled using non-linear relationships between meteorological variables and available CO <sub>2</sub> fluxes. The network is trained by presenting it with sets of regulating meteorological variables and available CO <sub>2</sub> data to predict missing data.	Good performance particularly when data can be smoothed over trained networks

Good reliability of annual sum of the net CO<sub>2</sub> exchange refers to methods that ranked the best based on a several statistical metrics to predict annual fluxes as reported in References [122,123]. These statistical metrics include Root Mean Square Error, Bias Error and the annual CO<sub>2</sub> flux sum among others and were evaluated by comparing the filled NEE data with the observed values.

and ER in response to a variety of conditions [39–41]. A challenge with flux partitioning is introduced by the inhibitory effect of light on leaf respiration rates, known as the Kok effect [42]. In the light, autotrophic respiration can be significantly lower than at night resulting in GPP estimation errors when ignored [43].

Recent micrometeorological approaches have attempted to measure GPP using a sulfur-containing analog of CO<sub>2</sub>, carbonyl sulfide (COS) that acts as natural ‘tracer’ molecule for GPP. This molecule enters a leaf in the same manner as CO<sub>2</sub> and is broken down by the enzyme carbonic anhydrase. Because of this, COS ‘uptake’

**Table 5 Partitioning methods to estimate Gross Primary Productivity (GPP) and ecosystem respiration (Reco)**

Partitioning method	Description
Night-time method [124]	This method uses night-time NEE to estimate the basal Reco at 15 Celsius and the sensitivity of respiration to temperature. These parameters are then combined to estimate daytime Reco. GPP is estimated summing daytime Reco and daytime NEE values.
Day-time method [38]	This method uses daytime NEE to parameterize a light response curve, to calculate GPP. The fitted curve is used to estimate the basal Reco at 15 Celsius, and combined with a temperature response function, to estimate Reco.

Both methods assume that any difference between daytime and nighttime Reco is due to temperature alone.

should scale with GPP, removing the need for partitioning NEE into the GPP and respiration components [44]. Studies using this method are showing promising insights with GPP estimated using CO<sub>2</sub> vs. COS measurements agreeing within 15% in forests and crops [45]. Another study that investigated variability in COS uptake and release in forests found agreement to within 3.5% between the two methods when GPP was high [46]. These results suggest an opportunity to use indirect methods for assessing GPP at larger scales, although recent work also suggests that photosynthetic tissues are not the only sink for COS [46–48].

## Remote and proximal sensing

Obtaining photosynthetic carbon uptake measurements using gas exchange systems is laborious resulting in efforts to replace this technique with other high-throughput methods. There exists a rapid growth in plant phenotyping greenhouses with the goal of automated measurement capabilities [49] at scales ranging from leaf to globe (Figure 1). Even with the most modern technologies, direct monitoring of leaf or plant level gas exchange would require substantial effort and resources. Thus, there are emerging technologies that provide means to infer plant responses to their growth environments that overcome the limitation of gas exchange [50–53]. Commercial sensors are available that provide information about plant canopy architecture and volume, which is important to infer growth over time [54], yet disentangling the underlying factors that lead to this growth requires physiological understanding. In the field, plot-level estimations of photosynthetic traits have been successfully estimated using a variety of platforms [55–57]. However, there needs to be improvements to the precision, accuracy, repeatability, and data pipeline before we can use these methods to estimate photosynthesis. Nonetheless, these new methods have a large potential impact on leaf to canopy understanding of plant physiology, ecosystem functioning and improving breeding efforts to maximize crop yields. In this section, we will discuss emerging technologies to monitor photosynthesis using spectral reflectance or fluorescence techniques. We will first outline the tools used for these approaches followed by a description of how these tools are being used.

## Hyperspectral approaches to measure photosynthesis

Hyperspectral analysis is a non-destructive means of analysis that uses light reflected from vegetation to infer leaf, plant, canopy, or ecosystem performance. At the leaf and single-plant level, spectral sensors funnel light reflected from vegetation through a holographic diffraction grating, which separates light by wavelength across the electromagnetic spectrum [58]. Hyperspectral imaging data is in three ‘cubed’ dimensions with spectral wavelength ( $z$ ) across spatial co-ordinates ( $x,y$ ). Depending on the size of a single-pixel hyperspectral cameras can image vegetation from the whole plant to ecosystem scale [58].

Reflected light has become a powerful tool to characterize plant traits, including photosynthesis, given the varying response of light to leaf structure and pigment content at different wavelengths. In the near infrared (770–1300 nm), differences in chlorophyll and plant nitrogen content indicate a variety of vegetation stressors such as nutrient deficiency [59,60], plant disease status [61,62], and ozone damage [63], while the short wave infrared (SWIR1; 1300–2500 nm) indicates plant water status based traits [64,65]. In the past, discrete spectral reflectance indices were used as proxies for crop status [66]. However, computational and technological advances make it possible to derive photosynthetic capacities (maximum rate of carboxylation for C<sub>3</sub> and C<sub>4</sub> plants,  $V_{cmax}$  and  $V_{max}$ , respectively; and maximum rate of electron transport,  $J_{max}$ ) and make predictions about photosynthetic performance scaling from the leaf [67–71] to the plot [72,73] and ecosystem scales [74].

One significant advance is the commercial availability of high-resolution fiber optic leaf clip-attachments. Hyperspectral radiometers typically contain a radiometrically calibrated light source and standardized white and dark reference panels for calibration. Leaf-level reflective intensity is compared with the reference material. Computer models (discussed later) are then used to correlate portions of the leaf’s reflective spectrum with traditional measurements of gas exchange. Hyperspectral data can provide significant information about leaf photosynthesis at a fraction of the time compared with gas exchange [67–71,75]. These measurements can offer insight for upscaling to the plot level using field push carts [76] or drones mounted with hyperspectral cameras for breeding and research trials.

In addition to the hyperspectral methods mentioned above, recently handheld multispectral tools (e.g. FluroPen, Photo Systems Instruments, Drásov, Czech Republic; MultispeQ, PHOTOSYNQ INC. East Lansing MI, U.S.A.; and LI-600, LiCOR Biosciences Lincoln NE, U.S.A.) are used to monitor fluorescence and other parameters associated with leaves. Compared with hyperspectral leaf clips or fluorescence chambers sold with gas exchange units, these leaf tools can be used to more quickly and inexpensively screen for the vitality of photosynthetic systems

under biotic and abiotic stresses (e.g. [77]). Furthermore, these tools provide opportunity, in some cases, to specify wavebands of interest for specific phenotypes that can extend beyond photosynthetic measurements.

Inspired by the successful leaf-level estimations of photosynthetic capacities, hyperspectral imaging (HSI) techniques are increasingly applied to canopy-scale measurements [73,78]. Imaging hyperspectral spectrometers provide more spatial information than a leaf-clip portable radiometer. Because of this, these sensors are being utilized to reveal variability in photosynthetic traits of interest across leaves, plants, and/or over large geographic areas [72,74]. These HSI sensors can scan individual plants in a few seconds [79] or provide analysis spanning several km<sup>2</sup> if mounted on aircraft or Earth-orbiting satellites [80,81]. Compared with point-based portable radiometers, these HSI sensors result in the accumulation of large amounts of data that need to be processed in an innovative way.

To link reflectance spectra to photosynthetic physiological parameters, data processing pipelines must be tailored to specific sensing platforms. These data pipelines are critical to applications such as field phenotyping in a high-throughput manner. For leaf-level estimations of photosynthetic variables using reflectance spectra, great efforts have been made to select statistical techniques that can provide the best predictive power [75]. Partial Least Square Regression (PLSR) [82] is currently the most common technique used to relate reflectance spectra to photosynthesis associated parameters [68,71] due to its ability to reduce tens to hundreds of spectral bands to just a few orthogonal principle components (also known as latent variables). There are also other machine learning algorithms such as Artificial Neural Network (ANN)-based regression and Least Absolute Shrinkage and Selection Operator (LASSO) that have been used to estimate photosynthesis [83]. The availability of these machine learning and empirical algorithms also poses a dilemma regarding the most effective approach. Collectively harnessing the strengths of individual empirical or machine learning algorithms through regression stacking shows promise [72] although further studies are needed to test its effectiveness across more plant species. For estimations of photosynthesis using reflectance spectra at the plot and ecosystem levels, further data processing steps are necessary to account for spurious variations in reflectance caused by sun-target-sensor geometry, canopy structure, leaf scattering, atmospheric contaminations, and background soil [75]. These steps are required to ensure that only reflectance data associated with photosynthesis are used for estimations. Although Radiative Transfer Models (RTMs) such as PROSAIL [84] are developed to remove those spurious variations, few of them can be directly used in the proximal sensing setting [85]. However, these RTMs provide an alternative way to reduce hyperspectral data into several meaningful leaf traits, such as chlorophyll concentration, that can serve as a proxy for photosynthesis. For example, RTMs-inverted traits were shown to explain up to 60% of variation in photosynthetic physiology in a crop species [72].

Remote-sensing products that measure GPP are traditionally based on the Light-Use Efficiency (LUE) concept of ecosystem modeling [86] and empirical models that rely on the relationships between remote sensing-derived variables and GPP [87–90]. These methods provide reasonable estimates of GPP compared with measured EC fluxes, however, new emerging spectral sensing technologies including Solar-Induced chlorophyll Fluorescence (SIF) are providing potential for estimating GPP at the ecosystem scale [91–93]. A fraction of solar radiation absorbed by chlorophyll is emitted as fluorescence, hence SIF is more physiologically based than other traditional remote sensing products [94] as it is a direct product of the photosynthetic process [95–97]. While pulse amplitude modulated chlorophyll fluorescence has long been used to measure photochemical efficiencies and heat dissipation in individual leaves [98], this should not be confused with SIF, which relies on measuring of the radiance chlorophyll fluorescence from an ecosystem.

Passive SIF measurements were first applied at the satellite scale (Table 6) [99] to assess regional and global scale patterns of SIF alongside GPP [91–93] and is now being implemented at flux towers across multiple ecosystem types to determine the physiological and structural relationship between SIF and photosynthesis at this scale [100–103]. Likewise, the near-infrared radiance of vegetation index (NIR<sub>v</sub>) has shown promising accuracy at detecting photosynthetic variability at the hourly scale over crop and forest system [104,105]. Therefore, both SIF and NIR<sub>v</sub> should enable real-time monitoring of productivity and stress.

The relationship between SIF and GPP is primarily dominated by absorbed photosynthetic active radiation (APAR) [106,107], implying that the correlation between SIF and GPP is the highest when photosynthesis is primarily light-limited [108,109]. However, GPP is also controlled by environmental factors other than light, and recent insights suggest that SIF responded to environmental stresses in a similar way as GPP, encouraging the application of SIF to estimate photosynthesis [94]. A relationship between SIF and GPP was similar among ecosystems although the relationship was stronger for grasslands than forests, savannas and croplands, and for



**Table 6 Spatial and temporal resolution major satellite sensors and platforms for Solar Induced Photosynthesis (SIF) estimations**

Sensors/Satellites	Status	Spatial resolution (km × km)	Temporal resolution	Sampling strategy	Spatial coverage
Thermal and Near-infrared Sensor for carbon Observations — Fourier Transform Spectrometer (TNSO-FTS)/Greenhouse Gases Observing Satellite (GOSAT)	In operation since 2009	10 × 10	3 days	Sparse	Global
Global Ozone Monitoring Experiment-2 (GOME-2)/Metop satellites	In operation since 2007	80 × 40 (40 × 40 <sup>1</sup> )	29 days	Continuous	Global
SCanning Imaging Absorption SpectroMeter for Atmospheric ChartographY (SCIMACHY)/Envisat satellite	2002-2012	200 × 30	2 days	Continuous	Global
TROPOspheric Monitoring Instrument (TROPOMI)/Sentinel- 5p	In operation since 2017	7 × 3	1 day	Continuous	Global
Orbiting Carbon Observatory 2 instrument/OCO-2	In operation since 2014	1.3 × 2.25	16 days	Sparse	Global
Orbiting Carbon Observatory 3 instrument/OCO-3	In operation since 2019 at International Space Station	1.75 × 2.2	Not fixed	Sparse	Global
Fluorescence Imaging Spectrometer (FLORIS)/Fluorescence Explorer (FLEX)	In planning for 2022	0.3 × 0.3	27 days	Continuous	Global

<sup>1</sup>The spatial resolution 40 by 40 km is available since July 2013 in Metop-A and B tandem operation;SIF measurement was first applied at the satellite scale [99] to assess regional and global scale patterns of SIF alongside GPP [91–93]. Currently, it is being implemented at flux towers across multiple ecosystem types to determine the physiological and structural relationship between SIF and photosynthesis at this scale [100–103]. For comparison, the EC method has a spatial resolution between hundred meters and several kilometers, and a continuous temporal resolution (half-hour) with a fine spatial coverage at the ecosystem and landscape scales.

C4 grasslands and crops than C3 ecosystems [94]. This quasi-universal relationship indicates that SIF could be a valuable tool for inferring GPP of the land surface. More collaborative studies between the EC and remote sensing communities are needed to evaluate why the relationship between SIF and GPP varies among ecosystems and under differing environmental conditions to improve the ability of SIF products to estimate ecosystem GPP robustly to scale regionally and globally.

Much progress has been made to understand the relationship between SIF and GPP but many challenges remain [109–111]. Higher spatial and temporal resolution SIF measurements are needed to coincide with the continuous GPP measurements [112]. Promising solutions to these challenges would be to develop remote sensing approaches that can cross-calibrate and blend multi-source SIF and reflectance measurements for a consistent record in both spatial and temporal domains. For example, combining satellite SIF with satellite reflectance was used to generate a spatially and temporally continuous SIF dataset [113]. Another solution is to improve SIF sensor designs to facilitate measurements at a much higher spatial and temporal resolutions. For example, the Fluorescence Imaging Spectrometer (FLORIS) onboard the Fluorescence EXplorer (FLEX) satellite can provide SIF at a better spatial resolution than its predecessors (Table 6) [114] and the newly launched Orbiting Carbon Observatory 3 instrument (OCO-3) allow for more coverage globally at higher definition [115].

## Conclusion

Interestingly, much of the work on remote sensing has initiated with large-scale measurements, yet there is a tremendous need to increase throughput of measurements at leaf and plot scales, particularly for application in high throughput phenotyping facilities. Whether these techniques are fully scalable remains uncertain, yet the opportunity for multidisciplinary research has advanced the versatility of the tools outlined in this review beyond their original users. Moving forward, simplifying data collection through ‘turn-key’ sensors and

standardizing data analysis pipelines for the variety of techniques outlined here are certain to advance understanding of plant function from molecular to global scale.

## Summary

- Monitoring Photosynthesis at every scale, from leaf to ecosystem, is an important task given the challenges of climate change and growing human populations.
- In the past 5 years there have been significant improvements to the technology and computational tools used to measure photosynthesis at every scale. And new facilities and equipment are being used around the world to monitor photosynthesis.
- Hyperspectral imaging at the leaf, and canopy scale paired with improved computational modeling allows for rapid estimates of important biochemical parameters.
- Micrometeorological approaches to estimate Gross Primary Productivity have been improved by the uses of sulfur tracing elements.
- Monitoring Solar Induced Fluorescence is a promising satellite-based method that should enable real-time monitoring of global ecosystem productivity.

## Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

## Author Contribution

M.H.S., N.G.-C., and C.J.B. conceived the outline, all authors contributed to the organization and writing of the manuscript, M.H.S. and N.G.-C. Edited the manuscript, and C.J.B. supervised the project.

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## Abbreviations

COS, carbonyl sulfide; EC, eddy covariance; ER, ecosystem respiration; FLEX, fluorescence explorer; FLORIS, fluorescence imaging spectrometer; GPP, gross primary productivity; HSI, hyperspectral imaging; NEE, net ecosystem exchange; RTMs, radiative transfer models; SIF, solar induced fluorescence.

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