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Widespread inhibition of daytime ecosystem respiration

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Abstract

The global land surface absorbs about a third of anthropogenic emissions each year, due to the difference between two key processes: ecosystem photosynthesis and respiration. Despite the importance of these two processes, it is not possible to measure either at the ecosystem scale during the daytime. Eddy-covariance measurements are widely used as the closest 'quasi-direct' ecosystem-scale observation from which to estimate ecosystem photosynthesis and respiration. Recent research, however, suggests that current estimates may be biased by up to 25%, due to a previously unaccounted for process: the inhibition of leaf respiration in the light. Yet the extent of inhibition remains debated, and implications for estimates of ecosystem-scale respiration and photosynthesis remain unquantified. Here, we quantify an apparent inhibition of daytime ecosystem respiration across the global FLUXNET eddy-covariance network and identify a pervasive influence that varies by season and ecosystem type. We develop partitioning methods that can detect an apparent ecosystem-scale inhibition of daytime respiration and find that diurnal patterns of ecosystem respiration might be markedly different than previously thought. The results call for the re-evaluation of global terrestrial carbon cycle models and also suggest that current global estimates of photosynthesis and respiration may be biased, some on the order of magnitude of anthropogenic fossil fuel emissions.

Introduction

The eddy-covariance technique allows for the measurement of the exchange of carbon between ecosystems and the atmosphere at a high temporal (that is, half-hourly) frequency[1]. Since the 1980s the technique has been widely deployed, and is currently used to measure land–atmosphere exchange of carbon, water and energy at hundreds of sites around the world[2].

The net measured flux of carbon (F_c) is the result of two contrasting processes: the uptake of carbon through photosynthesis and the release of carbon through ecosystem respiration. Night-time respiration is observed directly at the ecosystem scale using eddy-covariance, but daytime photosynthesis and respiration are mixed in the measured daytime net F_c flux. A variety of approaches have therefore been developed to estimate both the apparent photosynthesis (true photosynthesis minus photorespiration[3], F_p) and ecosystem respiration (F_r) from the measured net F_c (for example, refs. [4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22]).

The partitioned estimates of F_p and F_r have been combined with machine learning to generate data-driven budgets of global photosynthesis and respiration (for example, refs. 23,24), allowing for new understanding of the controls of global ecosystem function and the carbon cycle (for example, ref. 25). They are also widely used to test and develop process-based models[26] and remote-sensing-based estimates of ecosystem function[27].

Recent evidence, however, suggests that a key overlooked process may affect the partitioned estimates of F_p and F_r: the inhibition of leaf respiration in the light[28,29]. Leaf respiration is an important component of plant function[30] and often accounts for 50% of whole plant respiration[31]. Leaf level studies have long suggested that leaf respiration is inhibited in the light[32], although the responsible processes remain unclear[32,33,34], but the lack of evidence at the ecosystem scale has historically limited research to theoretical explorations of the potential impact on estimates of apparent photosynthesis and ecosystem respiration[3,6,11,22,35,36,37,38,39]. Importantly, in the absence of ecosystem-scale evidence[12,19], methods used to partition eddy-covariance have assumed that ecosystem-scale respiration is not inhibited by light. Recent isotopic evidence[28,29,40] suggests that this is no longer a tenable assumption, and that considerable biases result in the two main approaches used to partition eddy-covariance observations of F_c[12,19]. However, evidence for an ecosystem-scale inhibition of leaf respiration in the light across a variety of ecosystems, and an assessment of implications for the two main partitioning approaches to estimate F_p and F_r, remains lacking[29,41].

There are two main approaches to partition measured eddy-covariance measurements of F_c into the component fluxes of F_p and F_r. The night-time method[12] relies on the fact that fluxes measured during the night consist of purely F_r (as photosynthesis requires light). The night-time method uses measured night-time fluxes to estimate a seasonally varying reference respiration rate (R_{ref}, at a reference temperature) and the sensitivity to temperature (for example, refs. 6,12,42,43,44,45,46). These parameters, estimated from night-time data, are then combined to estimate F_r during the day. The difference between the observed F_c and the estimated F_r gives an estimate of F_p ($F_c = F_r - F_p$). In contrast, the second approach, referred to as the daytime method[19], uses primarily daytime data, and estimates F_p by fitting a light-response curve to observations of F_c[7,9,15,19,44,47]. The fitted curve, informed by daytime measurements, is used to estimate R_{ref} and, combined with a temperature response function, to estimate night-time F_r fluxes. Importantly, both the daytime and night-time methods assume that any difference between daytime and night-time ecosystem respiration is due to temperature alone[12,19].

An inhibition of leaf respiration during the day would affect both the daytime and night-time partitioning approaches[12,19], but it would do so in different ways for each. The approach focused on night-time data[12] assumes that F_r responds solely to temperature and thus increases with temperature

during the day. The night-time method will thus overestimate daytime total ecosystem respiration, and consequently apparent photosynthesis (Fig. 1), if leaf respiration is inhibited during the day[11]. Similarly, the approach focused on daytime data[19] assumes that the difference between daytime estimated F_r and F_r at night is driven solely by temperature. The daytime method will thus underestimate night-time respiration if inhibition occurs (Fig. 1). Fundamentally, both methods assume that the same R_{ref} is applicable during the daytime as at night; this is a questionable assumption due to the potential for the inhibition of leaf respiration in the light (for example, refs. 11,32).
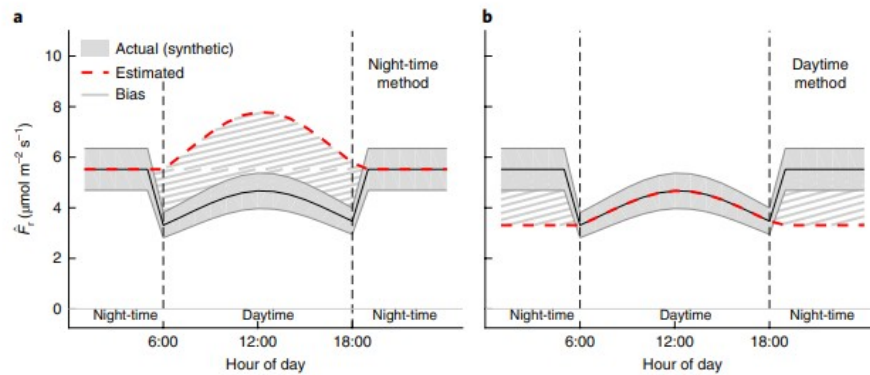

Fig. 1 | A schematic representation of the potential bias due to a hypothetical inhibition of reference respiration (R_{ref}) between night-time (R_{ref}^N) and daytime (R_{ref}^D). a,b, Biases are estimated for ecosystem respiration (F_r) from the night-time partitioning method (**a**) and the daytime partitioning method (**b**), using synthetic values for ecosystem respiration ($\hat{F}_r$). Grey areas represent the observed flux and red lines the flux predicted by the night-time (**a**) and daytime (**b**) methods. Cross-hatched areas indicate biases. Vertical lines represent the times of hypothetical sunrise and sunset.

Here, we use globally distributed eddy-covariance observations from the FLUXNET 2015 dataset[2] to develop data-driven estimates of an apparent inhibition of ecosystem-scale respiration during the day. Employing multiple methods, we estimate reference respiration separately during the day (R_{ref}^D) and during the night (R_{ref}^N), and use the difference between them as an estimate of the apparent inhibition of daytime ecosystem respiration. Our analysis indicates a widespread occurrence of inhibition, which follows consistent seasonal patterns within ecosystem types, with magnitudes that differ by ecosystem type, and is in line with reports of a leaf-level inhibition of non-photorespiratory mitochondrial CO_2 release in the light. We assess the implications for estimates of F_p and F_r, and suggest two modified algorithms that detect and account for inhibited daytime respiration.

Results

We found reference ecosystem respiration estimated using the daytime method to be consistently lower than reference respiration estimated using only night-time observations (Fig. 2a) during the growing season. Apparent ecosystem inhibition, defined as $100 \times (R_{ref}^N - R_{ref}^D)/R_{ref}^N$, showed a marked ecosystem-type-specific seasonal pattern. For example, at Harvard Forest, a deciduous

forest in the northeastern United States, the apparent inhibition of total ecosystem respiration reached 30% during the spring, dropping off to near zero shortly after peak foliage development (Fig. 2a), which is consistent with a previous isotope-based study at this site[29] although larger than suggested by expectations based on leaf-level results (see Supplementary Information). We observed a similar seasonal cycle at other deciduous broad-leaved forests (Fig. 2b), with maximum apparent inhibition in early spring. The seasonal cycle in evergreen needle-leaved forests was elongated compared to deciduous forests and less pronounced in spring, and had a lower overall level of apparent ecosystem-scale inhibition (Fig. 2b). Evergreen broad-leaved forests showed low apparent ecosystem-scale inhibition levels (Fig. 2b), potentially in contrast with reports of a consistent 30% inhibition across tropical and Mediterranean broad-leaved species at the leaf level[48,49]. This suggests that either non-leaf respiration contributes a large proportion of ecosystem respiration in evergreen broad-leaved ecosystems, or we underestimate the impact of leaf-level inhibition on an ecosystem scale for evergreen broad-leaved forests. In general, the seasonal cycle of apparent inhibition generally matched the seasonal cycle of satellite-derived fraction of absorbed photosynthetically active radiation (fAPAR) (Supplementary Fig. 1), indicating a large influence of active leaf area.
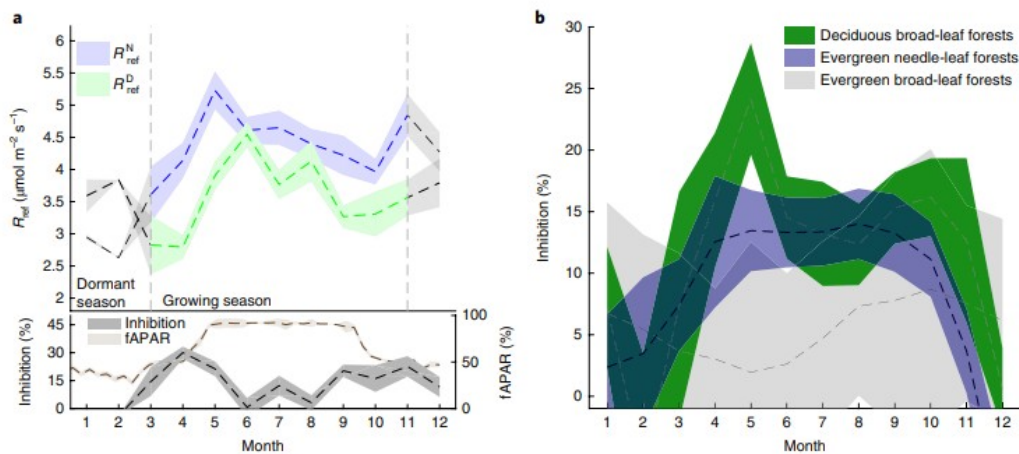
Fig. 2 | Seasonal cycles of R_{ref} inferred from both day- and night-time observations. a, Mean monthly estimates of R_{ref} from daytime (R_{ref}^{D}) and night-time (R_{ref}^{N}) data (Harvard Forest, 1992–2015, top), and the resulting estimate of mean monthly inhibition (%) (calculated as $100 \times (R_{ref}^{N} - R_{ref}^{D})/R_{ref}^{N}$, bottom panel), along with the satellite-derived mean monthly fAPAR (2001–2015). Vertical lines separate the growing season from the dormant season. Shaded areas represent the standard error about the mean monthly values. **b,** Mean monthly inhibition for three different PFTs, deciduous broad-leaf forests (n=12), evergreen neede-leaf forests (n=25) and evergreen broad-leaf forests (n=5) using Tier 1 sites with 5 years or more in the FLUXNET database. Shaded areas represent the standard error about the mean monthly values.

The extent of apparent inhibition differed by ecosystem plant functional type (PFT, Fig. 3) with mean apparent inhibition levels during the growing season ranging from 22.9 ± 3.7% (mean ± s.e.m.) for open shrublands to a low of 5.1 ± 3.8% for evergreen broad-leaved forests (Fig. 3). The PFTs with largest apparent inhibition (open shrublands, savannahs, woody savannahs and wetlands, Fig. 3), also showed the highest bias in F_r between partitioning methods in a previous study19. Over all sites, the average apparent
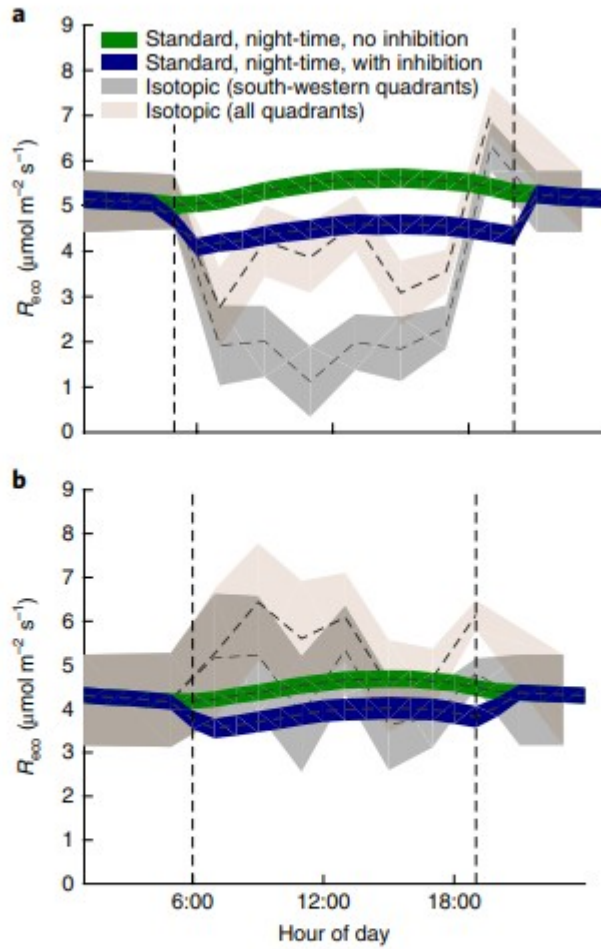
inhibition of ecosystem respiration during the growing season estimated by the modified daytime partitioning method was 14.4 ± 1.9%, which was lower than the 19.8 ± 1.7% we estimated from the independent generalized additive models (GAM) approach (Supplementary Fig. 2), but consistent with a hypothetical extrapolation of a range of estimates of the inhibition of leaf-level respiration in the light to the ecosystem scale (Supplementary Methods 1).
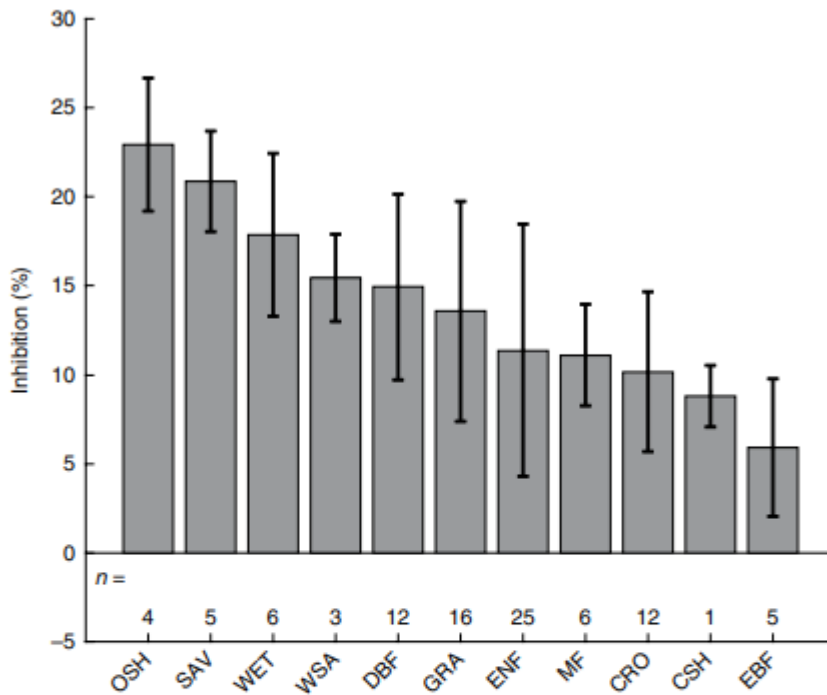
Fig. 3 | Mean inhibition (I, %) during the growing season for each of 11 different ecosystem types. Inhibition values are calculated as $100 \times (R_{ref}^{N} - R_{ref}^{D})/R_{ref}^{N}$ (that is, as the relative difference between R_{ref} during daytime, R_{ref}^{D}, and night-time, R_{ref}^{N}) for different PFTs for sites with a data record of 5 years or more. SAV, savannah; GRA, grassland; DBF, deciduous broad-leaved forest; ENF, evergreen needle-leaved forest; MF, mixed forest; OSH, open shrubland; WSA, woody savannah; CSH, closed shrubland; CRO, cropland; EBF, evergreen broad-leaved forest; WET, wetland. Error bars represent the s.e.m. across sites, while n represents the number of sites for each PFT.

We assessed the detected apparent inhibition by comparing our estimates of F_r to independent estimates obtained from multi-year isotope records at Harvard Forest29. The apparent inhibition at Harvard Forest implied a lower rate of F_r during the daytime than at night, particularly in late spring and early summer (Fig. 4a). The temporal dynamics in F_r largely matched those inferred by isotope measurements29 when using observations from all wind directions. The isotopic observations show a larger apparent inhibition when filtered for the south-western quadrant (Fig. 4a, as in ref. 29), which is a

more homogeneous region, dominated by deciduous trees. The lack of agreement for a particular wind direction is not surprising: the night-time and daytime partitioning methods are parameterized using all directions, as limiting to a specific direction limits the data available for parameterization, whereas the relative abundance of deciduous versus evergreen trees differs by wind direction[29]. Differences in the predominant wind direction during the daytime and night-time have also been suggested to potentially cause differences in apparent inhibition levels[29], although we did not find meaningful differences in the predominant wind directions between day and night at Harvard Forest (Supplementary Fig. 4). Late summer fluxes also showed evidence of apparent inhibition in the eddy-covariance flux data, in contrast to results from the isotopic data. It should be noted, however, that changes in flux footprints could potentially lead to meaningful differences between the isotopic and eddy-covariance methods.

Fig. 4 | A comparison of the standard night-time partitioning, with and without inhibition, to the partitioning inferred from carbon isotope measurements at Harvard Forest. a,b, Ecosystem respiration (F_r) for the June–July (**a**) and August–September (**b**) periods. The carbon isotope inferred fluxes are those presented in Wehr et al.[29]. Shaded areas represent one standard error about the mean.
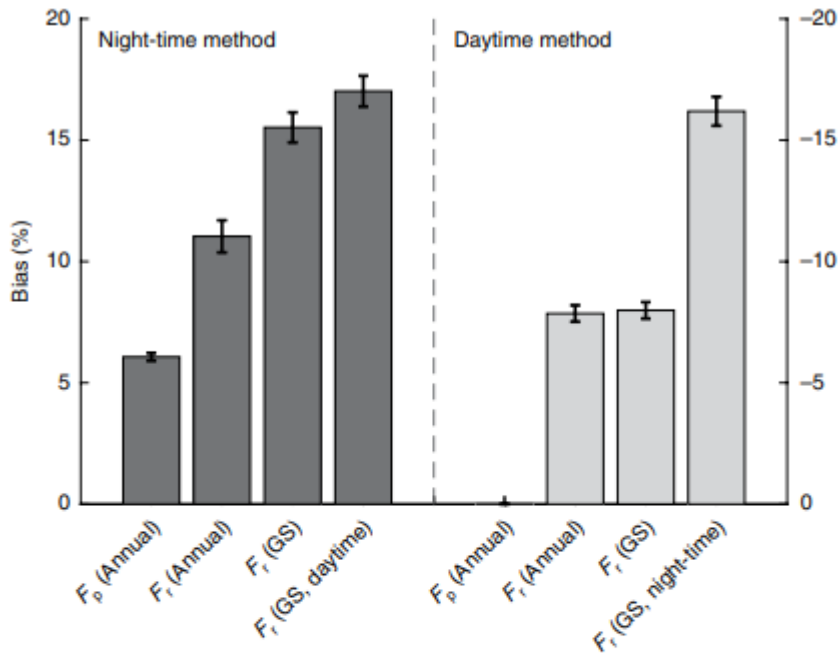
Fig. 5 | Relative biases in estimates of photosynthesis (F_p) and respiration (F_r). Biases are calculated on both an annual and growing season (GS) basis and for the growing season during the day for the night-time method (GS, daytime) and during the night for the daytime method (GS, night-time). Biases (positive, left; negative, right) are defined for each method as the difference between the version of the method that does not allow for an inhibition of ecosystem respiration during the day and the version that does. Positive biases (left) indicate that the method version that does not allow for inhibition overestimates net flux components compared to the version that does allow for inhibition. Values are calculated using all data from the FLUXNET Tier 1 dataset. Error bars represent the s.e.m. bias across all sites.

The prevalence of apparent inhibition suggests that previous approaches to partition F_c into F_r and F_p are probably biased. We compared estimates of F_r and F_p from both the daytime and night-time partitioning methods, with and without the modifications that allow for an apparent inhibition of ecosystem respiration (see Methods). As expected, the daytime method showed no bias in F_p on any timescale (Fig. 5), as any bias introduced by light inhibition of leaf respiration in the daytime method would primarily affect the daytime method estimates of respiration at night (Fig. 1). Indeed, not taking apparent inhibition into account in the daytime method led to an underestimation of total annual F_r by 7.9 ± 0.4% (Fig. 5). This bias was prevalent during the growing season only, and was due to a 16.2 ± 0.6% underestimation of growing season night-time F_r (Fig. 5, Supplementary Fig. 3). In contrast, for the night-time partitioning method, apparent inhibition led to positive biases, that is, an overestimation in both F_p and F_r. Biases in F_p, which by definition occur during growing season daytime

conditions, led to an overestimation of total annual F_p by 7.0 ± 0.2%. Total annual biases in F_r of 11.4 ± 0.7% were primarily due to an overestimation of 17.4 ± 0.6% during growing season daytime conditions (Fig. 5).

Discussion

The lack of evidence of the influence of the inhibition of leaf respiration in the light on canopy-scale processes has led to much debate and allowed ecosystem models and eddy-covariance partitioning methods to omit the process altogether[11,32,38]. Recent results using isotopic flux observations[29,41], however, have confirmed that ecosystem-scale respiration was often lower during the day at two sites, and the response was attributed to the inhibition of leaf respiration in the light. In a study at a deciduous temperate forest[29], F_r was more than two times lower during the day than at night in the early growing season. This difference was not captured by the non-isotopic partitioning approaches tested, leading to an overestimation of ~25% of apparent photosynthesis in spring at that forest. Similarly, a short campaign of isotopic flux observations in an alfalfa field[41] found lower F_r during the day, and subsequently a bias in the partitioning methods tested. Our results suggest that inhibition is indeed a pervasive phenomenon, but one that varies in magnitude by season and PFT. The resulting biases are smaller than previously reported[29], particularly at annual scales (Fig. 5), but have important implications for diel cycles, partitioning methods and ecosystem models.

The seasonal cycle of apparent inhibition we report is in line with previous results showing that apparent inhibition is stronger in the early growing season at Harvard Forest[29]. One explanation for such a dynamic is found in the relative contribution of above-ground and below-ground respiration to the total respiratory flux. At Harvard Forest, for example, the early season respiratory flux is ~50% above-ground respiration, driven by leaf growth and development, compared to a value of 10% later in the growing season, when soil respiration plays a larger role[50]. This is consistent with reports that leaf respiration is highest in late spring and decreases during the course of the summer[51,52], due to higher metabolic activity associated with development of new leaves and shoots[52]. Seasonality of apparent inhibition at the ecosystem scale is probably influenced by multiple factors, such as, in particular, the seasonal changes in the ratio of leaf to branch, stem and soil respiration[11,38,53,54], seasonal changes in the components of foliar respiration (that is, the fact that the construction costs of new leaves is higher in spring[55,56]), increases in the proportion of soil respiration due to priming by root exudates and increases in the shaded leaf fraction with canopy development[57]. Consistent with the latter, an influence of total leaf area has also been proposed[11,38] and is supported here by comparisons to seasonal cycles of fAPAR (Supplementary Fig. 1), with higher leaf area potentially leading to higher leaf respiration and thus a higher influence on apparent inhibition. That said, higher leaf area can be associated with denser forests with high soil and woody biomass and respiration rates[58,59], and we did not

observe a relationship between maximum fAPAR and apparent inhibition across sites. This suggests that the distribution of apparent inhibition across PFTs is more related to the ratio of leaf to non-leaf respiration than to total leaf area. Measurements of seasonal cycles of leaf-level inhibition of leaf respiration in the light across a variety of plant types, along with measurements of non-leaf (soil, roots, bole and branch) respiration rates, would help explain the seasonality and between-site inhibition differences reported here.

Other factors, unrelated to the actual leaf-scale process, could also affect the apparent difference between daytime and night-time respiration reported here. Night-time observations are often associated with low and sporadic turbulence, and although the observations are processed to minimize the effect of low turbulence, other forms of transport (for example, advection) may bias the observed fluxes[17]. However, advective losses of CO_2 would result in an underestimation of night-time fluxes (and thus R_{ref}^N) and consequently an underestimation of inhibition. Advective losses are highly site dependent, but intercomparison experiments using eddy-covariance fluxes and upscaled chamber estimates suggest an underestimation of night-time respiration by up to 30% (refs. 60,61,62). Similarly, the boundary layer can become stratified at night due to radiative cooling of the canopy, with an associated increase in storage of respired CO_2 within the canopy[63]. Increases in turbulence in the early morning can cause vertical advection[64], as is commonly observed in sites with more complex canopy structure (for example, ref. 65), which could lead to an overestimation of apparent R_{ref}^D and thus an underestimation of apparent inhibition. These potential biases, along with results of the independent GAM method and synthetic analyses (Supplementary Fig. 2), suggest that the levels of apparent inhibition reported here represent a conservative estimate. Other potential biases, such as the choice of temperatures for partitioning (for example, air, leaf, wood and soil temperatures[53,54]), also deserve further attention. The single source models used here, however, have the potential to be over-parameterized[12,19], so an approach that adds more parameters for ecosystem components at different temperatures and sensitivities is unlikely to be widely applicable[53].

An additional source of uncertainty lies in the fact that the temperature sensitivity of non-photorespiratory mitochondrial CO_2 release has been reported to be lower during the day than at night[66,67]. We assessed the implications of a lower leaf E_0 for our results by rerunning the partitioning and analysis with a lower E_0 imposed for daytime respiration, setting a conservative[66] ratio of night-time to daytime leaf of $E_0^d\_leaf = 0.5 \cdot E_0^n$. To scale to ecosystem respiration, we assumed that leaf respiration is 50% of total ecosystem respiration. There is considerable variation in this scaling ratio between sites, but 50% represents a conservative estimate for Harvard Forest[50] and temperate forests more broadly. The results show that applying

a lower $E_0^d\_leaf$ leads to only small changes in the magnitude of the detected response. At Harvard Forest, for example, the apparent inhibition is reduced in the August–September period, but not in June–July (Supplementary Fig. 6), and the reduction does not affect the general magnitude of inhibition or its seasonal cycle at this site (Supplementary Fig. 7). Across all sites globally, using the lower E_0 for leaf daytime respiration leads to a small reduction in the bias between methods (Supplementary Fig. 8). $E_0^{d\_leaf}$ could also vary seasonally due to acclimation, although there is little consensus regarding whether and how $E_0^{d\_leaf}$ acclimates. For example, McLaughlin et al.[68] report long-term acclimation of the temperature response of $E_0^{d\_leaf}$ in one species but not in another. Other studies also report seasonal acclimation[69,70,71], but many studies report no acclimation between seasons[72,73]. Most recently, Heskel et al.[74] found no seasonal variation in the temperature sensitivity of daytime leaf respiration for the dominant species (Red Oak) at Harvard Forest. Crous et al.[75] conclude that it is not known whether or by how much $E_0^{d\_leaf}$ varies seasonally under field conditions, and they hypothesize that the difference between study results may reflect a species-specific ability to acclimate and may be restricted to fast growing species.

Ultimately, independent measurements of each ecosystem respiration and temperature component, and photosynthesis proxies, are needed to reduce uncertainty in current estimates of apparent photosynthesis and respiration at eddy-covariance sites. A full characterization of the uncertainties involved will require the incorporation of multiple alternative partitioning approaches and assumptions.

Neither the night-time- or daytime-based partitioning algorithms most commonly used account for the inhibition of respiration during the day. Previous results suggest that this omission would lead to a 10 to 25% overestimation of daily apparent photosynthesis at specific sites[11,29,41]. Here we show that the implications are more nuanced, at times in the opposite direction to that previously suggested, and depend on the partitioning method used. The daytime method showed no effect of inhibition on estimates of either apparent photosynthesis or daytime respiration, but did underestimate respiration at night (Fig. 5). In contrast, both apparent photosynthesis and respiration estimates from the night-time method were biased by the apparent inhibition, leading to an overestimation of both. The mean growing season bias in respiration during the day or night in the night-time and daytime methods (respectively, 17.4 ± 0.6%, –16.2 ± 0.6%, mean ± s.e.m., Fig. 5) is in line with published estimates of inhibition at the leaf scale[38] (Supplementary Methods 1). The annual biases we report are

comparable to previous analyses of methodological bias. For example, Falge et al.[44], using different methods and a limited number of sites, reported an annual respiration bias of ~6% between different daytime and night-time partitioning approaches, whereas both Suyker and Verma[7] and Xu and Baldocchi[76] report a bias of up to 20%, compared to our reported average bias of 9.7% (Fig. 5). Lasslop et al.[19], however, reported a small median bias in annual ecosystem respiration of $13\,g\,C\,m^{-2}\,yr^{-1}$ between the daytime and night-time methods, compared to our median biases of -43.4 ± 0.08 and $77.7 \pm 0.2\,g\,C\,m^{-2}\,yr^{-1}$ for the daytime and night-time methods, respectively.

As both the night-time and daytime methods are commonly used by upscaling approaches to estimate global budgets of photosynthesis and respiration (for example, refs. 23,24), our results suggest a bias in previous global estimates based on eddy-covariance data. That said, although biases were relatively high at certain times of the year (for example, during the day in the growing season in the night-time method; during the night in the daytime method), annual totals were less affected. Our estimates suggest that annual apparent photosynthesis was overestimated by the night-time method by an average of $7.0 \pm 0.2\%$ at the studied sites, and annual respiration overestimated by $11.4 \pm 0.7\%$. For the daytime method, the only biases were for respiration, ranging from $16.2 \pm 0.6\%$ for night-time respiration during the growing season to $7.9 \pm 0.3\%$ on an annual scale.

Although the most commonly used night-time and daytime methods do not account for a lower basal respiration during the day, both can be modified to allow them to do so. In the case of the daytime method[19], the modification is relatively straightforward (see Methods). Our results suggest that future partitioning efforts should include a modified daytime method, where R_{ref}^{N} is used to estimate respiration during the night, not R_{ref}^{D}. In the case of the night-time method[12], accounting for inhibition requires an independent estimate of R_{ref}^{D}. Here we use a fitted light-response curve to estimate the R_{ref}^{D} applied in the modified night-time method. Note that this approach, to an extent, preserves the original distinction between the night-time and daytime methods. The original night-time method uses only night-time observations, while the original daytime method uses primarily daytime observations but also uses night-time observations to estimate the temperature sensitivity of ecosystem respiration (E_0, equation (1)[19]). Here, the modified daytime method additionally uses night-time observations to estimate R_{ref}^{N} and the modified night-time method uses daytime observations to estimate R_{ref}^{D}. As with the original night-time method, the modified night-time method estimates F_p as the residual between observed F_c and modelled F_r. The modified daytime method preserves the approach of the original daytime method by estimating F_p as a function of light, temperature and vapour pressure deficit. It is worth noting, however, that the modified methods proposed here, as with the original daytime method, do not

preserve full independence between night-time and daytime data, which could lead to self-correlation (see ref. 77).

To assess the robustness of our results, we developed an independent machine learning approach (see Methods) to estimate R_{ref}^{D} and R_{ref}^{N} using GAMs[78]. The strength of such an inductive approach is that it does not require the functional form of the response to be specified a priori, thus reducing the influence of model structural error, which is known to lead to biases in estimates of R_{ref}^{D} (refs. 9,79). Estimates of apparent inhibition from the GAM method were larger than those from the modified daytime and night-time methods, suggesting that the results presented herein may be conservative estimates of ecosystem-scale inhibition. Being unconstrained, however, the GAM approach can lead to implausible responses (for example, a negative quantum yield of photosynthesis) if such responses are supported by the observations for specific windows. Although the GAM method used here is therefore not readily applicable for partitioning eddy-covariance flux observations, advanced applications of machine learning methods to flux partitioning (see, for example, refs. 13,16,41) may prove effective.

Our results have potentially important implications for models of the terrestrial carbon cycle. Few such models include an inhibition of leaf respiration in the light and those that do lack the information necessary for adequate parameterization[32,38,80], although previous studies have tested the potential bias implicated[11]. Eddy-covariance observations are commonly used to develop and test all other estimates of ecosystem-scale photosynthesis and respiration (for example, land surface models and remote sensing). We show that the fluxes of respiration and apparent photosynthesis previously used were incorrect, with biases that vary on both diel and seasonal cycles. The biases uncovered here thus probably apply to land surface models and remote-sensing-based estimates of photosynthesis and respiration.

The inhibition of leaf respiration in the light has long been acknowledged[32], and is supported by various lines of evidence[38] and estimation techniques[32], although different interpretations exist regarding the actual mechanisms involved[32,33,34,81,82]. Tcherkez et al.[32] summarize various explanations for the inhibition of leaf respiration in the light and conclude that it is probably due to a combination of different processes. Previous studies have suggested that the inhibition may also affect ecosystem-scale fluxes[22,29,41]. Here, we demonstrate that ecosystem basal respiration is systematically lower during the day than at night in a wide variety of ecosystem types. The observed apparent inhibition is consistent with previous reports of leaf-level inhibition of respiration in the light, although we do not identify the underlying cause. The results suggest that previous eddy-covariance-based estimates of global photosynthesis and respiration are probably biased high, and call for a re-evaluation of terrestrial ecosystem models.

Methods

Eddy-covariance observations

We used eddy-covariance observations of carbon fluxes between ecosystems and the atmosphere from the FLUXNET 2015 openly available (Tier 1) database. The database contains observations from 166 sites around the world (Supplementary Table 1, www.fluxnet.org), incorporating data collected at sites from multiple regional flux networks. The data used include half-hourly or hourly observations of net carbon fluxes (F_c) and meteorological observations (incoming radiation SW_IN_FILL, air temperature TA_F and vapour pressure deficit VPD_F). All analysis was performed on data that were pre-filtered by the FLUXNET network to exclude conditions of low turbulence or conditions that do not meet the requirement of the eddy-covariance technique. The F_c estimate used was NEE_VUT_USTAR50, which applied a variable threshold of friction velocity (USTAR) for each year from the 50th percentile of USTAR thresholds identified. The associated uncertainty estimate used is NEE_VUT_USTAR50_RANDUNC. All data used are freely available for download, along with detailed descriptions, at http://fluxnet.fluxdata.org/.

Partitioning methods

We applied the two most commonly used partitioning methods, one focused on the use of night-time data[12] and the other primarily focused on the use of daytime data[19]. Here we describe both methods as applied, and then describe the modifications made to each to allow the detection and incorporation of an apparent inhibition of respiration in the light.

Night-time partitioning method

The night-time partitioning method relies on the fact that photosynthesis is zero at night, so any night-time measurements purely contain the respiratory flux. The night-time method uses night-time measurements to estimate a reference respiration rate, which is then projected into the day using a temperature response function that is directly parameterized by night-time observations[12]. The difference between this estimate of daytime respiration (F_r) and the observed net carbon flux (F_c) is then attributed to apparent photosynthesis (F_p). Formally, the model is constructed using an Arrhenius-type model after Lloyd and Taylor[83] to describe the temperature dependence of F_r as

$$F_r = R_{ref} \exp\left[E_0 \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{air} - T_0} \right) \right] \tag{1}$$

where R_{ref} ($\mu mol\, C\, m^{-2}\, s^{-1}$) is the reference respiration rate at the reference temperature ($T_{ref} = 15\,°C$) and E_0 (°C) is the temperature sensitivity. T_{air} is the air temperature and the parameter T_0 (°C) is set to a constant –46.02 °C following Lloyd and Taylor[83]. A constant value is estimated for E_0 for the

whole year, while R_{ref} is estimated every 5 days using a 15-day window (following ref. 12). Here, $R_{ref} = R_{ref}^{N}$. It should be noted that the true driving temperature is probably a combination of air, leaf, wood and soil temperatures[53,54]; the approach applied here follows convention in using air temperature observations, as those are most commonly available across a wide range of sites. The night-time method is thus applied to partition the observed flux data from the FLUXNET 2015 Tier 1 data release (Supplementary Table 1), and the R code implementation is available to download from https://github.com/bgctw/REddyProc (ref. 84).

Daytime partitioning method

The daytime partitioning method differs from the night-time partitioning method in that it uses observations during the daytime to parameterize a light-response curve, from which it estimates both the reference respiration R_{ref} and the photosynthetic carbon flux (F_p). Night-time data are also used in the daytime method, but only to estimate the temperature sensitivity parameter E_0. Formally, the net carbon flux (F_c) is modelled following Lasslop et al.[19] using a combination of the rectangular hyperbolic light-response curve[8] and an ecosystem respiration term[9] as

$$F_c = \frac{\alpha \beta R_g}{\alpha R_g + \beta} + \gamma \qquad (2)$$

where α ($\mu mol\,C\,J^{-1}$) is the canopy-scale quantum yield (that is, the initial slope of the light-response curve), β ($\mu mol\,C\,m^{-2}\,s^{-1}$) is the maximum rate of CO_2 uptake of the canopy at light saturation, R_g is the global radiation ($W\,m^{-2}$) and γ ($\mu mol\,C\,m^{-2}\,s^{-1}$) is the modelled ecosystem respiration (described below). Parameter β is estimated as an exponentially decreasing function of atmospheric vapour pressure deficit of air (VPD), to account for the effect of VPD on apparent photosynthesis:

$$\beta = \begin{cases} \beta_0 \exp(-k(VPD - VPD_0)), & VPD > VPD_0 \\ \beta_0, & VPD \leq VPD_0 \end{cases} \qquad (3)$$

where β_0, k and VPD_0 are fit parameters.

The modelled respiration term, γ, is estimated using the same function as in equation (that is, $\gamma = Fr\gamma = Fr$). Here, E_0 is first estimated as in the night-time method, by fitting equation 1 to night-time observations. With the fixed E_0, the remaining parameters (R_{ref}^{D}, α, β_0, k and VPD_0) are estimated by fitting the entire model (equation 2) to the daytime data. Night-time fluxes of F_r are then estimated by using the fit model (with R_{ref}^{D}, α, β_0, k and VPD_0 from daytime data and E_0 from night-time data) along with the observed night-time air temperatures. The daytime method is thus applied to partition the observed flux data from the FLUXNET 2015 Tier 1 data release, and the R

code implementation[84] is available to download from https://github.com/bgctw/REddyProc. In both the daytime and night-time methods, day and night were determined based on the corresponding flags in the FLUXNET data archive (that is, variable NIGHT).

Modified partitioning methods that allow for inhibition

Both of the approaches described above are built on the assumption that the reference respiration rate (R_{ref}) does not change between night and day (that is, $R_{ref}^{N} = R_{ref}^{D}$). The night-time approach applies an R_{ref} that is estimated using night-time data to the daytime, and the daytime approach applies an R_{ref} that is estimated using primarily daytime data to the night-time. Clearly, if the reference respiration rate is lower during the day than during the night, as has been suggested by recent studies[29,41], then the night-time method will overestimate daytime respiration (and thus by definition apparent photosynthesis) and the daytime method will underestimate night-time respiration.

We modified both the standard daytime and night-time partitioning methods[12,19] described above to account for an apparent inhibition by estimating and applying R_{ref}^{N} and R_{ref}^{D} separately. Here, we describe the modifications performed and their motivation.

For the modified daytime method, we changed the implementation to allow for a difference between the reference respiration that is applied to estimate night-time and daytime fluxes. The standard daytime method estimates R_{ref}^{N} and uses it as a prior to estimate R_{ref}^{D}. It then uses R_{ref}^{D} to estimate both night- and daytime respiratory fluxes. In our modified daytime method we applied R_{ref}^{D} to estimate daytime fluxes only and applied R_{ref}^{N} to estimate night-time fluxes. Otherwise, the modified daytime method preserves the structure of the original daytime method, with both F_r and F_p estimated by equations 1 and 2, with parameters E_0 and R_{ref}^{N} estimated from night-time data and parameters R_{ref}^{D}, α, β_0, k and VPD$_0$ estimated from daytime data. To test the efficacy of the modified daytime methods, we compared the estimates of F_r from both the original and modified daytime method to observed night-time F_r (Supplementary Fig. 3).

For the modified night-time method, we similarly changed the implementation to allow for a difference between the reference respiration that is applied to estimate night-time and daytime fluxes. The standard night-time method estimates R_{ref}^{N} from night-time data and applies this R_{ref}^{N} to calculate daytime F_r. In our modified method, we used the night-time method derived R_{ref}^{N} to estimate night-time fluxes, as in the original method, but used an independently derived R_{ref}^{D} to estimate daytime fluxes. The R_{ref}^{D} used in the

modified night-time method is calculated following the same procedure as in the daytime method, based on the intercept of a light-response curve fit to daytime observations. Otherwise, the modified night-time method preserves the structure of the original, with F_r estimated by equation 1, and F_p taken as the residual between the observed F_c and the modelled F_r, with parameters E_0 and R_{ref}^N estimated from night-time data and parameters R_{ref}^D estimated from daytime data. These modifications largely preserve the original differences between the night-time and daytime methods but allow for an independent reference respiration to be used during the night and day in both the night-time and the daytime methods. It should be noted, however, that the modified night-time method is not solely based on night-time data, as daytime observations are used to estimate the daytime reference respiration based on the fit of a light-response curve.

Estimating apparent inhibition

We estimated apparent inhibition (I) as the difference between R_{ref} calculated separately from night-time (R_{ref}^N) and daytime (R_{ref}^D) observations. To ensure internal consistency, both R_{ref}^N and R_{ref}^D were estimated using the daytime method, as the prior (night-time-based) and posterior (daytime-based) estimates of R_{ref}. This implies that the same temperature sensitivity (E_0) and data window lengths are applied to both R_{ref}^N and R_{ref}^D for estimating I. We then estimated the percentage apparent inhibition from the estimated parameters on a monthly basis as $I = 100 \times (R_{ref}^N - R_{ref}^D)/R_{ref}^N$. Note that we implicitly assume that I is independent of light level as I is typically observed to start at very low light levels[32], although a dependence on light level has been reported[85].

Independent test based on GAMs

We developed an approach based on GAMs to derive independent estimates of R_{ref}^N and R_{ref}^D, and thus apparent inhibition, to compare with the inhibition estimates derived from the partitioning approach described above. GAMs are a form of generalized linear model in which the predicted variable depends on smooth functions of predictor variables, thus allowing for unprescribed non-linear responses[78]. We derived estimates of R_{ref}^N by fitting a GAM every second day to 12-day moving windows of night-time observations, using air temperature as a predictor. The GAM for estimating R_{ref}^N used penalized regression smoothing splines with a basis dimension of n knots (that is, fit < – gam($y \sim s(x, k = n)$), where x is the time series to be fit and s is a gam function parameter that implies the use of spline-based smooths). We estimated R_{ref}^N as the GAM prediction at given a reference temperature of the

mean hourly temperature of each window. Similarly, for R_{ref}^{D}, we fit a GAM every second day to 12-day moving windows of daytime observations, using air temperature, light and VPD as predictors. Here, the GAM used penalized regression smoothing splines with a basis dimension of 3, 5 and 3 knots for air temperature, light and VPD, respectively. The higher number of knots for the light response allowed the GAM to capture the non-linear form of the light-response curve. Only windows with 10 or more observations were used.

We then estimated R_{ref}^{D} as the GAM prediction at a given reference temperature of the mean hourly air temperature for each window, with zero light and window-mean VPD. The resulting apparent inhibition estimates were calculated as $I = 100 \times (R_{ref}^{N} - R_{ref}^{D})/R_{ref}^{N}$. The GAM analysis was implemented in R (version 3.3.3) using the Mixed GAM Computational Vehicle with Automatic Smoothness Estimation package (MGCV, version 1.8–23), with all parameters set to package defaults other than those specified here.

Satellite estimates of vegetation

As the inhibition of ecosystem respiration in the light is hypothesized to be driven by a suppression of leaf respiration[38], the presence of active leaf area can be useful to determine periods during which apparent inhibition might be expected. We used satellite estimates of fAPAR from the Moderate Resolution Imaging Spectroradiometer (MODIS) as a proxy for the extent of active leaf area. fAPAR estimates were obtained from the MOD15A2 fAPAR product at a 1 km resolution for a 3 × 3 pixel area around each site, on an 8-day temporal resolution for the period 1 March 2000 to 31 December 2015. These data were quality controlled and aggregated to monthly averages for comparison to the seasonal cycles of apparent inhibition across sites.

Reporting Summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Code availability

Code used in the analysis presented in this paper is available online in two repositories. The first contains the modified REddyProc partitioning algorithms and can be accessed at https://github.com/trevorkeenan/REddyProc. The second contains the post-partitioning data processing pipeline code and can be accessed at https://github.com/trevorkeenan/inhibitionPaperCode.

Data availability

This work used openly available FLUXNET 2015 v3 Tier 1 eddy-covariance data acquired and shared by the FLUXNET community. All related data is publicly available for download at http://fluxnet.fluxdata.org.

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