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Bringing the Kok effect to light: A review on the integration of daytime respiration and net ecosystem exchange

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Abstract. Net ecosystem exchange (NEE) represents the difference between carbon assimilated through photosynthesis, or gross primary productivity (GPP), and carbon released via ecosystem respiration (ER). NEE, measured via eddy covariance and chamber techniques, must be partitioned into these fluxes to accurately describe and understand the carbon dynamics of an ecosystem. GPP and daytime ER may be significantly overestimated if the light inhibition of foliar mitochondrial respiration, or "Kok effect," is not accurately estimated and further integrated into ecosystem measurements. The light inhibition of respiration, a composite effect of multiple cellular pathways, is reported to cause between 25-100% inhibition of foliar mitochondrial respiration, and for this reason needs to be considered when estimating larger carbon fluxes. Partitioning of respiration between autotrophic and heterotrophic respiration, and applying these scaled respiratory fluxes to the ecosystem-level proves to be difficult, and the integration of light inhibition into single and continuous measures of ecosystem respiration will require new interpretations and analysis of carbon exchange in terrestrial ecosystems.

Key words: eddy covariance; Kok effect; net ecosystem exchange; photosynthesis; respiration.

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INTRODUCTION

The flow of carbon between the land and atmosphere accounts for immense fluxes of carbon dioxide globally. These fluxes vary interannually and are influenced by human activity and climate patterns, resulting in the storage of 1–5 Pg C yr^{-1} in terrestrial systems according to recent model estimations (IPCC 2007, Le Quere et al. 2009). The tremendous exchange of carbon between the atmosphere and terrestrial ecosystems is driven primarily by photosynthesis and respiration, fixing atmospheric carbon dioxide (CO_2) into C compounds for structural use and energy metabolism, and converting C compounds into chemical energy for cell maintenance and growth and releasing CO_2 back to the atmosphere. However, there is a great discrepancy on how photosynthesis and respiration are treated in models of carbon

exchange: photosynthesis can be accurately predicted from a mechanistic model (C_3: Farquhar et al. 1980; C_4: Collatz et al. 1992), while respiration is often modeled as a function of temperature or foliar nitrogen (Ryan 1991, de Pury and Farquhar 1997), a set fraction of photosynthetic carbon gain (DeLucia et al. 2007), or based on estimates of multiple separate processes (Cannell and Thornley 2000).

Ecosystem respiration (ER), the process which returns fixed carbon to the atmosphere, accounts for a large portion of the terrestrial carbon cycle and can originate from heterotrophic and autotrophic sources (Trumbore 2006). Autotrophic respiration, specifically that of plants, represents approximately half of overall ER, with leaves contributing approximately half of whole plant CO_2 release (Amthor 2000). Net ecosystem exchange (NEE), the difference between the carbon acquired through photosynthetic fixation (gross primary productivity, GPP) and the carbon released through ER, can be measured through eddy covariance techniques (Baldocchi et al. 1988). While these methods allow for estimation of ecosystem scale CO_2 flux, partitioning and interpretation of this value is difficult and requires the consideration of multiple scales and environmentally sensitive processes (Chambers et al. 2004, Griffis et al. 2004, Gilmanov et al. 2007, Zobitz et al. 2008, Lasslop et al. 2010). Here, we present an important and often overlooked phenomenon that impacts plant carbon cycling—the light inhibition of foliar respiration—and urge for its incorporation in calculations of ecosystem carbon exchange.

Plant respiration can determine the net amount of carbon stored in an ecosystem (Valentini et al. 2000). However, rates of plant respiration are highly variable within ecosystems due to the sensitivity of respiratory metabolism to environmental variables such as temperature (Dungan et al. 2003, Atkin et al. 2005), canopy position (when considering foliar respiration; [Brooks et al. 1991, Griffin et al. 2001, Griffin et al. 2002, Tissue et al. 2002, Turnbull et al. 2003]), soil moisture (Illeris and Jonasson 1999, Turnbull et al. 2001), and seasonality (Law et al. 1999, Nordstroem et al. 2001, Wilson et al. 2001, Falge et al. 2002, Griffis et al. 2004, Kwon et al. 2009). Additionally, irradiance is known to have an inhibitory effect on foliar respiration rates (Kok 1948, Kok 1956, Ishii and Murata 1978, Sharp et al. 1984, Kirschbaum and Farquhar 1987, Atkin et al. 1997), known as the "Kok effect." This light induced inhibition of foliar respiration can account for a 25–100% reduction of respiratory rates at the leaf level (Ishii and Murata 1978, Brooks and Farquhar 1985, Kirschbaum and Farquhar 1987, McCashin et al. 1988, Villar et al. 1994, Kromer 1995, Villar et al. 1995, Hurry et al. 1996, Atkin et al. 1997, Atkin et al. 1998, Atkin et al. 2000, Wang et al. 2001, Shapiro et al. 2004, Heskel et al. 2012). Here, we discuss its influence at larger scales, specifically on ecosystem respiration, and in turn gross primary productivity and net ecosystem exchange. Neglecting to incorporate an accurate estimate of respiration in the light (R_L) could result in overestimations in both ER and GPP. Our paper addresses the measurement and partitioning of NEE into different fluxes of carbon dioxide, and suggests how R_L should be evaluated and incorporated into models of ecosystem carbon cycling.

Net Ecosystem Exchange and its Measurement

The difference between the fluxes of photosynthesis and respiration at the ecosystem scale is represented as NEE. NEE is measured directly and serves as the basis for the calculation of GPP, where GPP = NEE − ER. ER refers to ecosystem respiration, the combined fluxes of autotrophic respiration (R_A, the respiration of leaves, stems and roots) and heterotrophic respiration (R_H), largely from soil microorganisms. The value for NEE can be either positive or negative, denoting the measured ecosystem as a carbon source or a carbon sink, respectively. NEE can be measured by eddy covariance techniques or by smaller chamber measurements. Eddy covariance (EC) provides direct, continuous measurements of CO_2 fluxes between the terrestrial ecosystem and the atmosphere by measuring the covariance between changes in wind velocity and CO_2 mixing ratio (Baldocchi 2003, Baldocchi 2008), and allows for seasonal, annual and multi-year exchange estimates of NEE (Baldocchi 2003). However, EC requires specific physical and environmental conditions for accurate measurement, including flat terrain and relatively large and uniform vegetation distribution within the

tower footprint (Baldocchi 2003, Finnigan et al. 2003). When these conditions are not met, bias can accrue in the data, causing inaccuracies that must be considered and corrected (Baldocchi 2003). Over long periods of time, intermittent technical issues may create gaps in the data, but these can be filled using statistical and empirical models (Falge et al. 2001, Ruppert et al. 2006, Moffat et al. 2007). Due to the large scale, continuous, non-destructive, and accurate measurements, EC towers number in the hundreds across the globe and are often integrated into cross-site networks at the regional, continental and global scale (Baldocchi 2008). The chamber method determines NEE and ER of the enclosed area by employing an infrared gas analyzer to measure the CO_2 concentration within the chamber. Clear plastic chambers are used for NEE measurements, and then darkened to measure ER. Subtracting ER from NEE can then estimate photosynthesis within the chamber footprint (Griffis et al. 2000). From these estimates, values for NEE can be scaled upward when variables such as leaf area index (LAI) are known. The chamber method can be labor intensive, but allows for true replicates unlike EC, where there is often only a single tower at each measurement site. For both methods, difficulty lies in the interpretation of the CO_2 flux values. When GPP is calculated, in both cases using ER estimates, an accurate measure of respiration is crucial to understanding the whole system.

Respiration in NEE Models

Respiration, unlike photosynthesis, occurs in all living cells of all organisms at all times. Due to the complications of measuring foliar respiration in daylight, ER is usually only measured at night or in darkened chambers. ER measurement at night by EC methods can be error prone and lead to inaccurate estimates due to the suppression of turbulence at night when friction velocity is too low (Goulden et al. 1996). Daytime measurements of ER using darkened chambers can often lead to higher than expected estimates when scaled to the ecosystem level (Lavigne et al. 1997, Law et al. 1999, Bolstad et al. 2004, Wohlfahrt et al. 2005*a*), potentially due to transient increases in foliar respiration that often occur when illuminated plants are exposed to darkness (Xue et al. 1996, Atkin et al. 1998, Atkin et al. 2000, Gilmanov et al. 2007, Barbour et al. 2011). Given these issues, extensive study has gone into modeling ER to obtain indirect estimates of CO_2 efflux based on environmental parameters. To overcome the bias introduced by the low turbulence, some models estimate ER by making ecosystem-scale light response curves (Wohlfahrt et al. 2005*a*, Gilmanov et al. 2007, Lasslop et al. 2010). Using the corresponding irradiance and NEE measures, a hyperbolic curve is fitted to describe the relationship between CO_2 flux and light. From these data, the fitted curve can be extrapolated back to the *y*-intercept to estimate the CO_2 efflux in the absence of light (Falge et al. 2001, Suyker and Verma 2001, Griffis et al. 2003, Wohlfahrt et al. 2005*a*, Gilmanov et al. 2007, Jassal et al. 2007). To create this curve, many values of NEE from a wide span of irradiances are required. However, as these light levels correspond to different times of day or through a season, they must be standardized to control for the temperature response of ER. Reichstein et al. (2005) provide a thorough comparison of both aforementioned methods highlighting their advantages and drawbacks.

NEE models are often simplified in terms of the assumptions about the temperature dependence of autotrophic respiration. This can lead to inaccuracies though, as respiratory Q_{10} values are nonlinear, and using fixed values could lead to over- or under-estimation of ER over longer time scales (Tjoelker et al. 2001, Davidson et al. 2006, Xu et al. 2007), and temperatures experienced during the day are warmer than experienced at nighttime and represent a portion of the temperature response curve that does not necessarily correspond to night ER fluxes (Tjoelker et al. 2001). Another area of oversight in NEE models, and the focus of this review, is the failure to incorporate the light inhibition of foliar respiration. This observed phenomenon can substantially suppress daytime foliar respiration rates, and neglecting it can potentially lead to overestimations of GPP. Here, we address the known physiological basis of the light inhibition of respiration, its leaf-level measurement, and its potential ability to be scaled to the ecosystem.

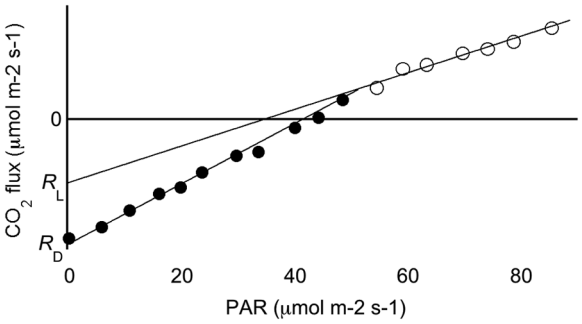

Fig. 1. A visualization of a low-light CO_2 assimilation curve depicting the Kok effect. At low PAR levels (below 100 μmol m^{-2} s^{-1}), a break in the linear light response curve occurs around the light compensation point. Points above the breakpoint (unshaded) are used to extrapolate a line to the y-axis which will yield the R_L estimate, whereas the measured data point when PAR = 0 will yield the R_D estimate.

The Inhibition of Respiration by Light

In the mid-20th century, Bessel Kok, using algal suspensions and aquatic plants, measured carbon assimilation as a response of light intensity and found a "sharp bend" at low light intensity, creating two distinct linear parts of the curve (Kok 1948, Kok 1949, Kok 1956). The two linear sections yield different intercepts on the y-axis (Fig. 1), which Kok interpreted to reveal the inhibitory effect of light and photochemical processes on respiration. The degree of this effect has been measured in many species through various techniques, and is reported to vary widely in degree of inhibition of mitochondrial respiration in the light (Ishii et al. 1979, Brooks and Farquhar 1985, Kirschbaum and Farquhar 1987, McCashin et al. 1988, Villar et al. 1994, Kromer 1995, Villar et al. 1995, Atkin et al. 1997, Atkin et al. 1998, Atkin et al. 2000, Wang et al. 2001, Warren et al. 2003, Shapiro et al. 2004, Hurry et al. 2005, Ayub et al. 2011, Crous et al. 2012, Heskel et al. 2012).

Research over the past half-century supports this inhibitory effect of light (Ishii and Murata 1978, Ishii et al. 1979, Sharp et al. 1984) and has identified a number of processes responsible for this phenomenon (Table 1). Multiple cellular pathways link photosynthesis and respiration directly and indirectly (Kok 1949, Raghavendra et al. 1994, Kromer 1995, Hoefnagel et al. 1998, Cournac et al. 2002, Riazunnisa et al. 2008), and many of these pathways serve as feedbacks to maintain efficient energy metabolism and avoid over-reduction or the accumulation of reactive oxygen species that can damage the cell (Saradadevi and Raghavendra 1992, Raghavendra et al. 1994, Forti 2008, Noguchi and Yoshida 2008). However, as a result of these overlapping processes, respiration rates are controlled and inhibited by light through gene regulation and associated enzyme and substrate concentrations (Hoefnagel et al. 1998, Rasmusson and Escobar 2007). Pyruvate dehydrogenase and malic enzyme, precursors to the tri-carboxylic acid (TCA)

Table 1. Identified causes of light inhibition of mitochondrial respiration: known mechanisms associated with respiration that are down-regulated in the light, causing an inhibitory effect. Locations of these processes and enzymes include the mitochondria (M), cytosol (C), choloroplast (CP), and peroxiosome (P).

Mechanism	Process	Location	Reference
Pyruvate dehydrogenase complex	Precursor to TCA cycle, catalyzes decarboxylation of pyruvate to acetyl CoA	M	Budde and Randall 1990 Tovar-Mendez et al. 2003
Malic enzyme	Oxidation of malate in the TCA cycle	M	Hill and Bryce 1992
Glycolysis	Produces pyruvate	C	Tcherkez et al. 2005, 2008
TCA cycle	Produces reductant	M	Tcherkez et al. 2005, 2008
ATP: ADP ratio	Available energy balance	C	Dry and Wiskich 1982 Peltier and Thibault 1985
Photorespiration	Oxygenation of RuBP, down-regulates TCA precursors	M, CP, P	Many, summarized in Hurry et al. 2005
Refixation†	CO_2 released from TCA cycle refixed by Calvin Cycle in stroma	M, CP	Loreto et al. 2001 Pinelli and Loreto 2003

† Refixation does not directly inhibit respiratory processes, but can produce an observable "inhibitory" effect due to the reduced CO_2 efflux from the leaf.

cycle, are both light inhibited (Budde and Randall 1990, Hill and Bryce 1992, Tovar-Méndez et al. 2003). Light is also linked to the reduction of glycolysis and reorganization of the TCA cycle (Tcherkez et al. 2005, Tcherkez et al. 2008, Tcherkez et al. 2012). As both photosynthesis and respiration produce energy in the form of adenosine triphosphate, this redundancy is thought to control R_L. While the ratio of cytosolic adenosine triphosphate to adenosine diphosphate (ATP:ADP) is related to the degree of inhibition of respiration, this is found to be true only at high values of this ratio (Dry and Wiskich 1982, Peltier and Thibault 1985).

Photorespiration, the oxygenation of ribulose-1,5-bisphosphate in the light, can be associated with the down-regulation of precursors to the TCA cycle and correlated with the degree of light inhibition of respiration (Budde and Randall 1990, Gemel and Randall 1992, Tovar-Méndez et al. 2003, Tcherkez et al. 2005). However, rates of respiration in the light may increase under increasing photorespiration, reflecting the demand for TCA cycle carbon skeletons associated with amino transfer reactions in the peroxisome (Tcherkez et al. 2008, Griffin and Turnbull 2013). Previous studies show that these processes may be compensatory, and the ratio of their rates can be sensitive to environmental factors such as ambient CO_2 concentration, irradiance, and temperature (Leegood et al. 1995, Pärnik and Keerberg 1995, Hurry et al. 1996, Hurry et al. 2005, Pärnik et al. 2007, Tcherkez et al. 2008). Photorespiration occurs concurrently with R_L and it can confound measurements using gas exchange techniques as both processes consume oxygen (O_2) and release CO_2.

Refixation, which occurs when the carbon released via mitochondrial respiration is reintegrated into photosynthetic processes, and thus not released into the atmosphere, can create a reduction in carbon efflux via respiration. Pinelli and Loreto (2003) found that respiration in the light was inversely related to photosynthetic rate, suggesting the refixation of emitted carbon (Loreto et al. 2001, Pinelli and Loreto 2003). At elevated CO_2, the respiratory CO_2 release in the light was lower than in plants exposed to ambient and low CO_2 levels, suggesting that optimal photosynthetic conditions of high CO_2 led to increased rates of intercellular CO_2 refixation and thus less efflux from the leaf to the atmosphere (Loreto et al. 2001, Pinelli and Loreto 2003, Busch et al. 2012). However, ^{14}C labeling experiments have shown that even when taking into account refixation, there is still true inhibition of the TCA cycle (Pärnik et al. 2007).

In addition to the cellular controls of the light inhibition of respiration, multiple studies identified environmental influences on the degree of this effect. Elevated CO_2 conditions can increase respiratory carbon loss in the light, and this may be further enhanced under higher measurement temperatures (Wang et al. 2001, Shapiro et al. 2004), and modified by seasonal timing and exposure to drought (Ayub et al. 2011, Crous et al. 2012). Warm conditions can affect the degree of inhibition of respiration across species (Heskel et al. 2013), and the warming effect can be further mediated by light conditions (Zaragoza-Castells et al. 2007) and the measurement temperature (Atkin et al. 2006, Ayub et al. 2011). Though leaves can exhibit minimal inhibition under high light conditions and cold measurement temperatures, suggesting the prioritization of metabolic efficiency under potentially stressful conditions, the degree of inhibition increases with leaf temperature, likely due to an increase of photorespiration at higher temperatures and the associated down-regulation of pyruvate dehydrogenase complex (Atkin et al. 2000, Zaragoza-Castells et al. 2007). Further, increased soil nutrient availability can relax the degree of inhibition of respiration in the light in multiple field-grown arctic (Heskel et al. 2012, Heskel et al. 2013) and rainforest species (Atkin et al. 2013), and in lab-grown *Xanthium strumarium* (Shapiro et al. 2004). Knowing these trends, the environmental sensitivity of the light inhibition of respiration needs to be further investigated to evaluate potential cross-taxa patterns that may inform larger-scale predictive carbon models.

Analytical models may also help elucidate the behavior of the biochemical mechanisms underlying the inhibition of respiration in the light. Buckley and Adams (2011), using a model based around flux-balance equations for cellular adenylate and reductant, found the suppression of respiration in light to be highly variable, controlled predominantly by photosynthetic ATP:ADP, and also arises when NADPH yield from the oxidative pentose pathway is limited.

Table 2. Simultaneous CO_2 and O_2 fluxes that occur in the light that can complicate direct measurement of R_L.

Process	Location	Consumes O_2	Releases CO_2
Mitochondrial respiration	Mitochondria	X	X
Photorespiration	Chloroplast stroma, peroxiosome, mitochondria	X	X
Chlororespiration	Thylakoid membrane	X	
Mehler Reaction	Thylakoid membrane	X	

This model supported findings from empirical study, mainly the inverse relationship of respiratory inhibition in the light with energy demand (Buckley and Adams 2011). This and hopefully additional future analytical models will expand the study of light inhibition of respiration through their theoretical insights. While plant biochemists and physiologists continue to reveal the direct and indirect causes of this inhibition at the cell level, ecophysiologists, ecosystem ecologists, and modelers can move forward in measuring the degree of this inhibition at different scales across ecosystems.

Measuring Respiration in the Light

Multiple O_2 and CO_2 fluxes occur concurrently in the light (Table 2), complicating direct measurement of respiration. However, methods have been developed in order to obtain estimates of R_L indirectly. These approaches vary in their methodologies, from the use of stable isotopes (Weger et al. 1988, Turpin et al. 1990, Pinelli and Loreto 2003), to radiocarbon (McCashin et al. 1988, Pärnik and Keerberg 1995, Hurry et al. 1996) and gas exchange (Kok 1948, Brooks and Farquhar 1985, Villar et al. 1994, Peisker and Apel 2001). Stable isotopes and radiocarbon techniques can be useful for the measurement of R_L, as they can determine pathway-specific rates of fluxes. While isotopic methods can reveal intricacies of metabolic pathways, they are not practical for larger scale observations that would be necessary for scaling up to the ecosystem level. For this reason, we will not consider these techniques here.

There are three primary methods for the detection of the Kok effect at the leaf level using gas exchange techniques: the Laisk method (Laisk 1977, Brooks and Farquhar 1985, Villar et al. 1995), the Peisker method (Peisker and Apel 2001), and the Kok method (Kok 1948, Sharp et al. 1984), though new methods are being developed, if not widely applied (Yin et al. 2011). Both the Laisk and Peisker methods utilize intercellular CO_2 concentration response (A-c_i) curves to estimate R_L. The Laisk method estimates the rate of R_L from the intersection of three A-c_i curves measured at different light levels. The intercellular CO_2 concentration at this point (c*) indicates where CO_2 assimilation is equal to the negative value of R_L ($A = -R_L$). The Peisker method estimates R_L and c* through linear regression of the CO_2 compensation concentration (Γ) and the product of the respiration rate in the dark (R_D) and the intercellular resistance for CO_2 fixation. Where the Laisk method assumes the degree of inhibition is independent of irradiance, the Peisker method assumes the degree of inhibition to be independent of R_D and photosynthetic performance (Peisker and Apel 2001).

The Kok method estimates R_L from CO_2 exchange values collected via infrared gas analysis within a cuvette when leaf material is exposed to decreasing light levels. Unlike the Peisker and Laisk method, the Kok method measures CO_2 exchange as a response of light, not intercellular CO_2 concentration. In the field, this aspect is highly important, as large differentials in CO_2 concentration between the gas exchange chamber and ambient air can further complicate measurements. At low light, or when values of photosynthetically active radiation (PAR) are less than 100 μmol m^{-2} s^{-2}, CO_2 uptake slows and eventually reaches the light compensation point (LCP). The LCP represents the PAR value where CO_2 efflux from respiration is equal to CO_2 consumption from photosynthesis. Around the LCP a breakpoint in the linear trend of CO_2 concentration occurs (Fig. 1). Extrapolating a line to the y-axis from the points above this breakpoint will yield a value assumed to be the amount of CO_2 respired in the light, whereas the y-intercept derived from the line created from the points below this breakpoint result in the dark respiration value (Fig. 1). Using

these two values, the degree of inhibition of respiration by light is calculable, where inhibition $= 1 - R_L/R_D$.

Of the gas exchange methods, the Kok method is the most practical protocol for multiple field-based measurements and allows for relatively simple analysis; both of these are required for broad-scale ecological surveys. It can be difficult to obtain the highly precise measurements of CO_2 fluxes needed to calculate the Kok effect in the field, though measures can be made to improve precision and general ease, including using cut leaves and transporting them in water to a well-ventilated, potentially temperature-controlled space for measurement, if available. Also, for scaling reasons, the Kok method is the only gas exchange method that could easily correspond with eddy covariance methods, as light and CO_2 flux are the only required parameters.

Integrating R_L into NEE Estimates

Few studies address the light inhibition of *R* and its implications for respiration estimates at the ecosystem scale (Falge et al. 1996, Falge et al. 1997, Janssens et al. 2001, Chambers et al. 2004, Yi et al. 2004, Reichstein et al. 2005, Wohlfahrt et al. 2005*b*, Bruhn et al. 2011). Of these, Chambers et al. (2004) reduced all daytime respiration estimates by 40% to account for this inhibition when partitioning carbon fluxes in a tropical forest system. Falge et al. (1996, 1997) reduced respiration in the dark by half in a stomatal conductance model to represent daytime respiration. Janssens et al. (2001), in a study that evaluated multiple sites across FLUXNET, a network of eddy covariance towers, approximated the overestimation of GPP by the neglect of the inhibition of respiration to be no more than 15%. These coarse estimations of R_L attempt to incorporate a physiological phenomenon whose underlying mechanisms are intricate and not well understood.

More involved integrations of the R_L into NEE estimation, like those by Wohlfahrt et al. (2005*b*) and Bruhn et al. (2011) may yield more accurate descriptions of ecosystem carbon cycling. Wohlfahrt et al. (2005*b*) applied the light inhibition of *R* to a model from EC flux measurements based in the Austrian Alps to estimate ecosystem GPP. Two estimates of the degree of inhibition were put into the model, 50% and 85%, corresponding to low and high light levels, respectively. The results yielded an 11–17% reduction in estimated GPP compared to models that did not incorporate the light inhibition of respiration (Wohlfahrt et al. 2005*b*). This study suggests that the degree of overestimation of GPP by neglecting this inhibitory effect is highly dependent on ecosystem attributes including the ratio of R_H to R_A and total leaf area in the measurement location (Wohlfahrt et al. 2005*b*).

Bruhn et al. (2011) scaled R_L to the ecosystem level by applying the leaf-level Kok method to NEE estimates measured through EC. CO_2 flux values were drawn from afternoon measurements where PAR was greater than the ecosystem LCP, but less than 550 μmol m^{-2} s^{-1} (Bruhn et al. 2011). Similar to foliar measurements, a line is fitted to these values and extrapolated to the y-axis to determine the estimate of ecosystem respiration in the light (ER_L). Ecosystem respiration in the dark (ER_D) was estimated using nighttime measurements of ER that were corrected to a constant temperature so they may be compared to ER_L values (Bruhn et al. 2011). While noting two different methods of estimating nighttime respiration (Falge et al. 2002, Lasslop et al. 2010), Bruhn et al. (2011) use nighttime ER estimates without mention of the potential error caused by low turbulence (Goulden et al. 1996). Effects of other sources of respiration (e.g., stem, root, soil) and light attenuation through the canopy were accounted for, resulting in a 52% and 82% inhibition of respiration (using each of the nighttime respiration estimates) when scaled to the canopy-level (Bruhn et al. 2011). Similarly, the authors note the environmental variability that occurs due to phenology and changes in soil moisture and canopy composition over longer time periods, and for this reason, warn against using blanket inhibition estimates (Bruhn et al. 2011). As these studies employ no new collection methodologies and only require new data analysis, further application should be pursued to evaluate potential specific environmental controls on light inhibition.

In addition to EC, a combined approach using stable isotope applications may reveal new information on ecosystem carbon release from leaves in the light. Foliar respiratory CO_2 release

in the light carries a different isotopic signature than that released in the dark; day respiration produces ^{13}C-depleted CO_2 likely due to the fractionation against ^{13}C by both pyruvate dehydrogenase and the TCA cycle, which may be further enhanced under light inhibition of those processes (Hurry et al. 2005, Tcherkez et al. 2005, Tcherkez et al. 2008). Tcherkez et al. (2010) found a slight ^{13}C depletion in CO_2 respired from leaves in the light compared to the ^{13}C-enriched respiratory release in the dark that could be identified at the mesocosm scale where it corresponded with isotopic fractionation measured in fluxes from a canopy of sunflower leaves in a growth chamber (Tcherkez et al. 2010). A logical continuation in terms of experimental application would be to test if the depleted ^{13}C signal of foliar respiration in the light could be detected in a less controlled environment, similar to the scaling of the enriched ^{13}C signal produced by light enhanced dark respiration from leaf to ecosystem at the leaf-level (Barbour et al. 2011). Though more experimentally intensive than EC measurement, stable isotope applications may allow for in situ direct quantification of foliar R_L in multiple species compared to the estimation of ER_L via EC, which cannot easily partition plant and soil sources of CO_2.

The studies above provide insight into the potential for the light inhibition of foliar respiration to be scaled and applied to the ecosystem level. However, it is necessary to realize that what holds true at the leaf level may not at the ecosystem level and an aggregate estimate of the degree of light inhibition of respiration of an ecosystem may not be easily scaled. Future research should consider the scaling properties of respiration and how environmental and species influences on the variation in light inhibition can be reconciled within and across different systems.

Implications and Conclusions

Neglecting to include the light inhibition of respiration can lead to overestimations of both GPP and ER (Amthor and Baldocchi 2001, Janssens et al. 2001, Morgenstern et al. 2004, Wohlfahrt et al. 2005*b*, Bruhn et al. 2011); as GPP is derived from ER, inaccurate assessments of ER will confound GPP. Including R_L (accounting for the Kok effect) into estimations for daytime ER will lead to more realistic approximations of carbon fluxes. Environmental variation will likely influence the degree to which the Kok effect impacts GPP estimates (Wohlfahrt et al. 2005*b*). For instance, in ecosystems that are mainly evergreen and can assimilate carbon year round, the R_L will have a larger influence on GPP estimates than ecosystems that only bear leaves for a portion of the year (Wohlfahrt et al. 2005*b*). This effect would also hold true in ecosystems that have a high R_A to R_H ratio, where ecosystem CO_2 efflux is more controlled by leaf respiration (Lohila et al. 2003, Wohlfahrt et al. 2005*b*). Conversely, for ecosystems with low leaf area index and where ER is dominated by soil respiration, the influence of the light inhibition of respiration on GPP may be minimal (Lavigne et al. 1997, Law et al. 1999, Janssens et al. 2001, Bolstad et al. 2004, Wohlfahrt et al. 2005*b*). In stands with high leaf area, self shading may limit this inhibitory effect for much of the canopy, dampening its effect on GPP (Wohlfahrt et al. 2005*b*).

For accurate estimates of both GPP and ER, the light inhibition of respiration must be integrated into evaluations of NEE. The Kok effect, detectable at the leaf level and responsible for varying degrees of respiratory inhibition, could have large implications for ecosystem scale carbon fluxes. Its measurement and application to the ecosystem scale will require new analysis and interpretation of eddy covariance measurements, along with the physiological 'ground-truthing' of foliar and chamber measurements at the individual and community levels across different environmental conditions.

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