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Review

Tansley insight

Estimating leaf day respiration from conventional gas exchange measurements

Xinyou Yin[1] **and Jeffrey S. Amthor**[2]

[1]Centre for Crop Systems Analysis, Department of Plant Sciences, Wageningen University & Research, PO Box 430, 6700 AK, Wageningen, the Netherlands; [2]Center for Ecosystem Science and Society, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

Authors for correspondence:
Xinyou Yin
Email: xinyou.yin@wur.nl

Jeffrey S. Amthor
Email: j-s-amthor@aya.yale.edu

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Summary

Leaf day respiration (R_d) strongly influences carbon-use efficiencies of whole plants and the global terrestrial biosphere. It has long been thought that R_d is slower than respiration in the dark at a given temperature, but measuring R_d by gas exchange remains a challenge because leaves in the light are also photosynthesizing. The Kok method and the Laisk method are widely used to estimate R_d. We highlight theoretical limitations of these popular methods, and recent progress toward their improvement by using additional information from chlorophyll fluorescence and by accounting for the photosynthetic reassimilation of respired CO_2. The latest evidence for daytime CO_2 and energy release from the oxidative pentose phosphate pathway in chloroplasts appears to be important to understanding R_d.

I. Introduction

Plant respiratory CO_2 efflux accounts for 30–60% of gross photosynthetic carbon assimilation (Amthor, 2010) and thus is an important determinant of carbon budgets and carbon-use efficiencies at scales from whole plants to the entire globe (Amthor, 2000; Tcherkez *et al.*, 2017). Leaf respiration accounts for a large fraction of whole-plant respiration (e.g. Lavigne *et al.*, 1997). Leaf day respiration (R_d) refers to the CO_2 release by processes other than photorespiration (Farquhar *et al.*, 1980) and differs from the respiration rate in the dark (R_{dk}) at a given temperature (Crous *et al.*, 2012). Quantifying R_d relative to R_{dk} therefore is important to understanding plant ecophysiology (e.g. Ayub *et al.*, 2011; Way *et al.*, 2019).

It is difficult to directly measure R_d by gas exchange because illuminated green cells are simultaneously photosynthesizing and respiring. Direct measurement of R_d relies on measurements of differences in the time courses of carbon isotope labelling of photosynthetic, photorespiratory, and respiratory intermediates with specialized equipment (reviewed by Tcherkez *et al.*, 2017). These methods can rely on somewhat uncertain assumptions, for example with regard to chloroplastic decarboxylation reactions (Tcherkez *et al.*, 2017). Estimating R_d together with other parameters of the C_3 photosynthesis model of Farquhar *et al.* (1980) by fitting data to full photosynthetic CO_2- and/or light-response curves measured by conventional gas exchange (e.g. Gregory *et al.*, 2021) is not recommended because R_d can be confounded by other parameters due to overfitting. The most common approaches to estimating R_d are the empirical Kok method (Kok, 1948) and the Laisk method (Laisk, 1977) that each use the low portion of photosynthetic light- or CO_2-response curves to constrain R_d. Here, we outline theoretical limitations of these methods, summarize how they can be improved, and consider implications of recent findings for previously unrecognized metabolic origins of R_d on its estimation.

II. The Kok method and the Laisk method

The Kok method exploits the Kok effect – the abrupt decrease in the linear slope of the relationship between net photosynthetic rate (A) at low but increasing incident photosynthetic photon flux density (I_{inc}; Fig. 1a). The Kok effect is apparent when A is measured as leaf CO_2-exchange (e.g. Buckley *et al.*, 2017) or O_2 production (Gauthier *et al.*, 2018). The decreasing slope with increasing I_{inc} has been interpreted as light inhibition of respiration, with the lower-slope extrapolation to zero I_{inc} yielding $-R_d$, which is smaller (less negative) than R_{dk} (Fig. 1a). Due to its simplicity, the Kok method is still used to estimate R_d (e.g. Way *et al.*, 2019; Faber *et al.*, 2022).

The Laisk method analyses linear responses of A to low intercellular CO_2 concentration (C_i) at multiple I_{inc} to find the common C_i at which the rate of photorespiratory CO_2 release equals the rate of CO_2 fixation. At this C_i, CO_2-release rate should equal R_d, which is the intersection point of A-C_i lines at two or more I_{inc} values (Fig. 2a; Supporting Information Methods S1, S2 give calculation methods that ensure a common-C_i solution). The Laisk method assumes that R_d is independent of I_{inc} and C_i within the ranges used. It has been criticized because measurements must be made at low CO_2 levels that are far from normal conditions (Tcherkez *et al.*, 2017) and an effect of CO_2 level on R_d has been reported (such an effect may, however, be an artifact of gas exchange system leaks, Amthor *et al.*, 2001). Since the Kok method underestimates R_d (to be described later), the Laisk method is often used (e.g. Atkin *et al.*, 2000; Crous *et al.*, 2013; Way *et al.*, 2019), even for nonsteady-state conditions (Schmiege *et al.*, 2023).

III. Exploiting chlorophyll fluorescence data to estimate R_d

Both Kok and Laisk methods are theoretically consistent with the electron transport-limited form of the C_3-photosynthesis model developed later by Farquhar *et al.* (1980):

$$A = \frac{(C_c - \Gamma_*)J}{4(C_c + 2\Gamma_*)} - R_d \qquad \text{Eqn 1}$$

where C_c is the CO_2 level in the chloroplast, Γ_* is the CO_2-photocompensation point in the absence of R_d, and J is the photosynthetic linear electron transport rate, which depends on I_{inc}. If C_c is constant while J varies proportionally with I_{inc} within the limiting-I_{inc} range, Eqn 1 indicates that the intercept of the

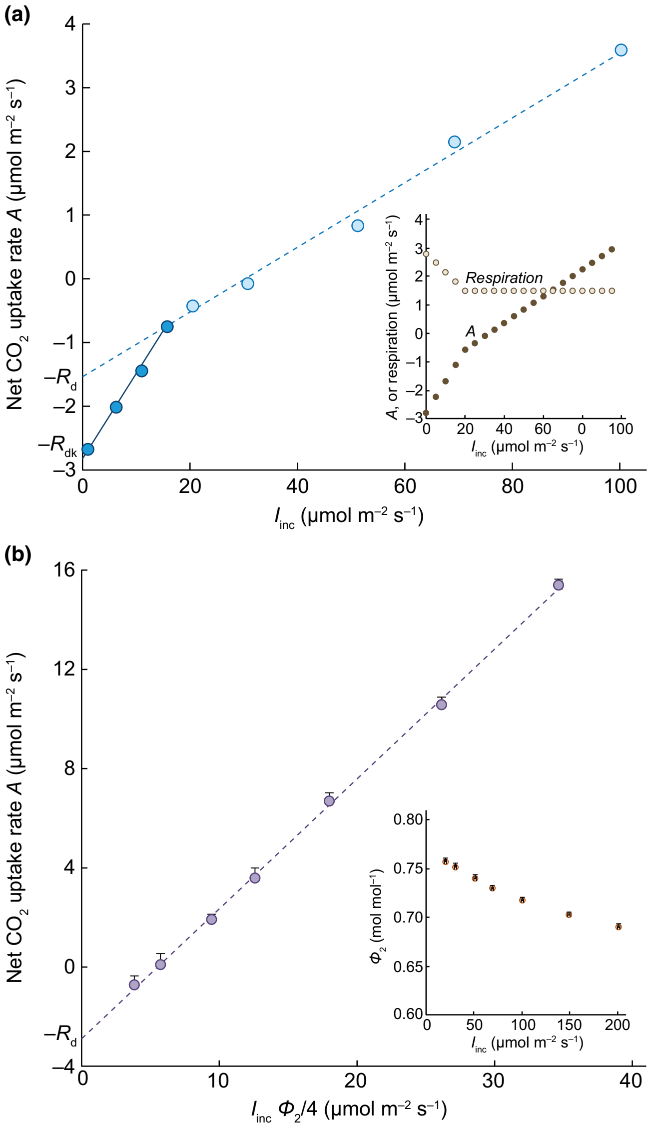

Fig. 1 Kok method and the Yin method. (a) Illustration of the Kok effect – a two-phase response of net CO_2 assimilation (A) to low incident photosynthetic photon flux density (I_{inc}) with the transition mostly occurring at I_{inc} around the light compensation point (i.e. I_{inc} corresponding to $A = 0$; redrawn from Yin *et al.*, 2020a). This effect was interpreted as an abrupt cessation of light suppression of respiration (see Yin *et al.*, 2020a; also as shown in the inset), resulting in the Kok method to estimate day respiration (R_d) with $-R_d$ as the intercept of the linear regression on the data above the transition or breakpoint (light-blue symbols). The intercept of the line below the transition point (dark-blue symbols) is close to the actual CO_2 exchange rate at zero I_{inc} – respiration rate in the dark (R_{dk}). (b) Illustration of the Yin method for estimation of R_d that accounts for the decline of Photosystem II (PSII) electron transport efficiency (Φ_2) with increasing I_{inc} (inset). The x-axis is changed from I_{inc} in the Kok method (panel a) to $I_{inc}\Phi_2/4$, where Φ_2 can be determined from chlorophyll fluorescence concurrently with gas exchange (error bars represent SEs). The intercept is $-R_d$. Further explanation of this figure can be found in Supporting Information Notes S1.

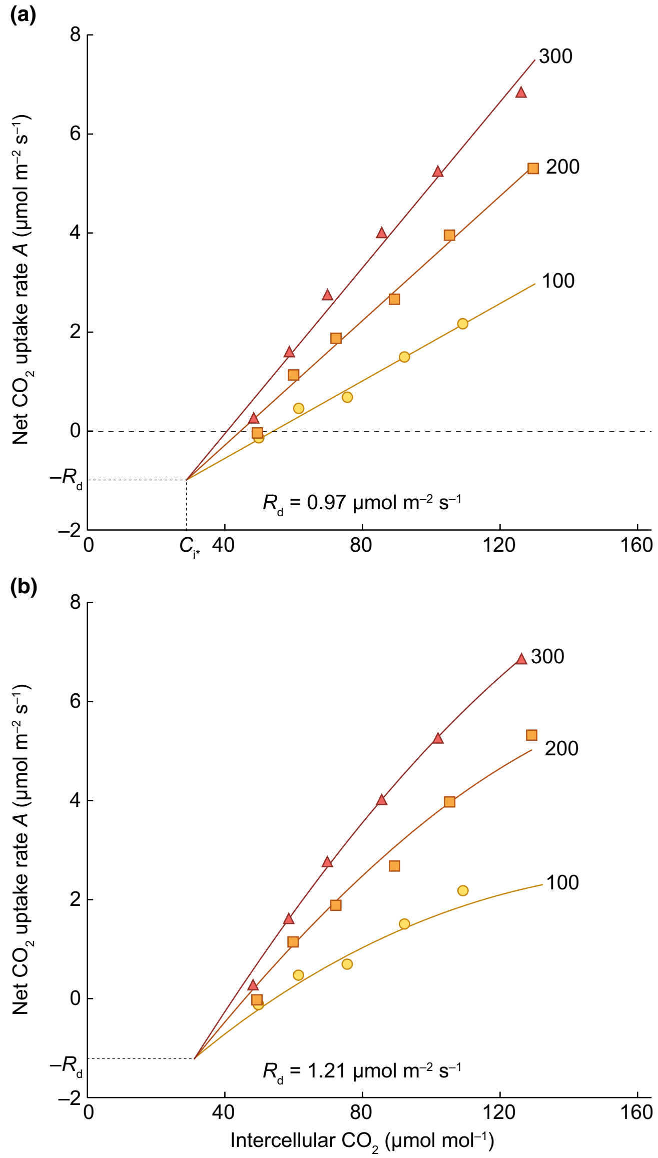

Fig. 2 Laisk method and the use of the nonrectangular hyperbolic equation for net CO_2 assimilation (the NRH-A method) to re-analyze data of the Laisk plot. (a) Illustration of the Laisk method to estimate day respiration (R_d) in which net CO_2-assimilation rates (A) are measured at low intercellular CO_2 levels (C_i) at two or more (typically three) incident photosynthetic photon flux densities (indicated by the numbers to the right of each line, in μmol m^{-2} s^{-1}; redrawn from wheat leaf measurements at 25°C; Yin *et al*., 2011). The estimated R_d was 0.97 μmol m^{-2} s^{-1} from the simultaneous fitting procedure of Yin *et al*. (2011); see Supporting Information Methods S1, S2 for this procedure). (b) Using the NRH-A method, Eqn 3, to re-fit the data of the Laisk plot to estimate R_d (gas exchange data are from Panel a). Curves are drawn from the fitted values of parameters of Eqn 3 giving $R_d = 1.21$ μmol m^{-2} s^{-1} and $g_m = 0.34$ mol m^{-2} s^{-1} (see Methods S3, S4 for the fitting scripts). Note that the Laisk plots are no longer linear. Further explanation of this figure can be found in Notes S2.

linear A-I_{inc} plot quantifies $-R_d$, similarly to the Kok method (Fig. 1a), and light progressively suppresses respiration only below the Kok-break point (Fig. 1a inset). Within the low CO_2-concentration range where A-C_c response curves are linear, Eqn 1 indicates that photosynthetic CO_2-response lines at two or more I_{inc} values meet at a common CO_2 level, that is Γ_*, and the point along the A-axis corresponding to Γ_* reflects $-R_d$, commensurate with the Laisk method (Fig. 2a).

The proportionality between A and I_{inc} assumed in the Kok method would mean that the photochemical efficiency of both photosystems (PS) is constant in the range of I_{inc} used. However, the quantum efficiency of PSII electron transport, Φ_2, as revealed by chlorophyll fluorescence, decreases with increasing I_{inc} (Fig. 1b inset). Since J can be replaced by $\Phi_2\rho_2\beta I_{\mathrm{inc}}$ (where β is absorptance by photosynthetic pigments and ρ_2 is the fraction of βI_{inc} associated with PSII), the Kok plot can be modified by plotting A against $\Phi_2 I_{\mathrm{inc}}/4$ (Yin *et al.*, 2009; Yin *et al.*, 2011). The intercept of this plot, which gives an estimate of $-R_d$ (Fig. 1b), has been called the Yin method (Tcherkez *et al.*, 2017; Schmiege *et al.*, 2023). Yin method estimates of R_d are *c.* 20% higher than Kok method estimates and are comparable with Laisk method values (Yin *et al.*, 2011).

IV. Considering reassimilation of respiratory CO_2

Both Kok and Yin methods use linear regression to estimate R_d, implicitly assuming that C_c is constant across light levels. Actually, C_c varies within the low range of I_{inc} used, even if the ambient-CO_2 level is constant (Farquhar & Busch, 2017), because the rapid CO_2 flux of respiration, relative to photosynthesis, at low I_{inc} drives CO_2 accumulation in the leaf against nonzero stomatal and mesophyll resistances. Using anatomical data combined with 2-D modelling accounting for CO_2 diffusion and reactions inside a leaf, Berghuijs *et al.* (2019) estimated R_d from gas exchange and chlorophyll fluorescence data and found that applying the Kok or Yin methods to photorespiratory conditions underestimated R_d. (Typical photorespiratory conditions are associated with ambient or subambient CO_2 levels and ambient O_2 level for C_3 species; nonphotorespiratory conditions can be obtained with high CO_2 and/or low O_2.) Theoretically, both Kok and Yin methods work for photorespiratory conditions only if C_c is constant across I_{inc}, which is difficult to achieve experimentally because stomatal conductance (g_s) and mesophyll conductance (g_m) are unknown beforehand. In fact, g_m-estimating methods can require R_d as input (Harley *et al.*, 1992).

If the 2-D reaction–diffusion modelling can estimate R_d (Berghuijs *et al.*, 2019), a simpler method, that is Eqn 1 coupled with a g_m-model, can also estimate R_d by fitting it to gas exchange and chlorophyll fluorescence data under photorespiratory conditions. CO_2 gradients along the bulk diffusional pathways are commonly described as:

$$C_c = C_i - A/g_m = C_a - A\left(\frac{1}{g_m}+\frac{1}{g_s}\right) \qquad \text{Eqn 2}$$

where C_a is the ambient CO_2 level outside the leaf. Combining Eqns 1, 2 gives a nonrectangular hyperbolic model describing CO_2 assimilation (NRH-A):

$$A = \frac{b-\sqrt{b^2-4c}}{2} \qquad \text{Eqn 3}$$

$$\text{with}\quad b = x_1 - R_d + g_m(C_i + x_2)$$

$$c = g_m[x_1(C_i - \Gamma_*) - R_d(C_i + x_2)]$$

where $x_1 = J/4$ and $x_2 = 2\Gamma_*$ (von Caemmerer, 2000). Based on this model, Farquhar & Busch (2017) showed that under photorespiratory conditions C_c sharply increased with decreasing I_{inc} (also see Fig. S1), meaning that respiration makes CO_2 substrate available for photosynthesis. Yin & Struik (2009) showed that this nonlinear NRH-A model, with J derived from chlorophyll fluorescence measurements on Φ_2 (Fig. 1b), can estimate g_m more reliably than the variable J method of Harley *et al.* (1992). Both the variable J method and the NRH-A method rely on accounting for the reassimilation of photorespired CO_2 to estimate g_m (Yin *et al.*, 2020b). The fraction of (photo)respired CO_2 being reassimilated can be calculated from stomatal and mesophyll resistance terms (Tholen *et al.*, 2012; Yin *et al.*, 2020b; Notes S3). Additionally, CO_2 released by (photo)respiration within a photosynthesizing cell decreases the chance of assimilating CO_2 from the ambient air. It is this net CO_2 reassimilation within a cell that the NRH-A model accounts for (Yin *et al.*, 2021).

Fang *et al.* (2022) showed that this NRH-A model can reliably estimate R_d and g_m simultaneously for photorespiratory conditions (see Methods S3, S4 for calculation methods) by exploring data across a range of low I_{inc} as in the Kok and Yin methods and that a NRH-A method with variable-g_m gave similar R_d estimates. They found that for wheat leaves under photorespiratory conditions, the Kok method underestimated R_d by *c.* 35%, whereas the Yin method underestimated R_d by *c.* 20%, indicating that in that case *c.* 20% of CO_2 released by respiration was reassimilated.

The NRH-A method for estimating R_d is analogous to applying the modified Kok method procedure of Kirschbaum & Farquhar (1987) to iteratively correct for the decrease in C_c with increasing I_{inc} (Ayub *et al.*, 2011; Crous *et al.*, 2012), but the NRH-A method is easier to implement and considers the Φ_2 dependence on I_{inc}. It is also analogous to the 2-D modelling of Berghuijs *et al.* (2019) that accounts for the reassimilation of (photo)respired CO_2, but with the benefit that the NRH-A model is considerably simpler than the 2-D model. The Kok and Yin methods are most accurate for nonphotorespiratory conditions because CO_2 reassimilation is then typically small (Yin *et al.*, 2020b; Notes S3).

We find that the NRH-A method can also be applied to analyzing Laisk plot data to simultaneously estimate R_d and g_m (Fig. 2b) if chlorophyll fluorescence data are also measured. Using the data in Fig. 2(a) combined with concurrently measured chlorophyll fluorescence data, the NRH-A method gave an estimate of R_d of 1.21 μmol m^{-2} s^{-1} (Fig. 2b), *c.* 25% higher than the value from the original Laisk method, indicating that the linear Laisk plot does not properly account for CO_2 reassimilation. This agrees with simulation results of Farquhar & Busch (2017) for underestimation of R_d by the Laisk method, and is compatible with the experimental estimate for reassimilation% (Busch *et al.*, 2013).

Box 1 Explaining the Kok effect, and the need to better elucidate respiratory CO_2 origins

The Kok method (Fig. 1a) attributes the Kok effect entirely to an inhibition of respiration by light. Other mechanisms co-contribute to the Kok effect (Tcherkez *et al.*, 2017; Gauthier *et al.*, 2020; Yin *et al.*, 2020a), including (1) the decline of Φ_2 and (2) the decrease of C_c (associated with CO_2-reassimilation) with increasing light intensity. Does light inhibition of respiration occur in the absence of these effects?

With optimally managed sunflower plants, Yin *et al.* (2020a) used Eqn 3 to disentangle Kok plots obtained at various levels of O_2, CO_2, and temperature and found that decreasing Φ_2 and C_c with increasing light intensity explained *c.* 12% and *c.* 25%, respectively, of the Kok effect. The remaining *c.* 63% was attributed to real light inhibition of R_d. Using wheat plants grown under various temperatures and water regimes, Fang *et al.* (2022) found that R_d estimated by Kok, Yin, and NRH-A (see text) methods was *c.* 60%, *c.* 72%, and *c.* 90% of R_{dk}, respectively, for normal photorespiratory conditions. Hence, the actual light inhibition of respiration was only *c.* 10%, agreeing with the estimate by Sun *et al.* (2023), who quantified the inhibition based on the same considerations as Fang *et al.* (2022) but relying on a separate method to pre-set R_d for estimating mesophyll conductance (g_m) first (see text). Differences among these studies quantifying actual inhibition of respiration could be due to different species or growth and measurement conditions.

Importantly, actual respiratory inhibition increases with increasing photorespiration rate (Yin *et al.*, 2020a; Fang *et al.*, 2022), implying changes in metabolic origins of R_d with changes in photorespiration. As such, simultaneous CO_2-release and O_2-uptake measurements (Hurry *et al.*, 2005; Posch *et al.*, 2022) and isotopic labelling of metabolites (e.g. Gauthier *et al.*, 2020; Wieloch, 2022) may be needed to identify changes in daytime respiratory substrates and reactions.

However, the percentage of reassimilation varies with conditions and species (Busch *et al.*, 2013; Yin *et al.*, 2020b), for which g_m also varies. The underestimation of R_d by Kok, Yin, and Laisk methods for photorespiratory conditions may vary with diffusional conductance (Fig. S1), and with the magnitude of R_d itself and other parameters.

V. The effect of metabolic origins of day respiration on its estimation

The above discussion indicates that real light inhibition of R_d is smaller than that estimated from the Kok method. However, real inhibition still appears to increase with increasing rates of photorespiration (Box 1), which calls for better insights about the metabolic origins of R_d and their dynamics.

We present various metabolic origins of R_d vs R_{dk} in Fig. 3, which highlights reactions/pathways that may differ between day and night and therefore regulate effects of light on respiration both quantitatively (rates of CO_2 production and substrate oxidation) and qualitatively (which substrates are converted to which products). Of various reactions, those occurring in chloroplasts are particularly relevant to estimating R_d, as the daytime CO_2

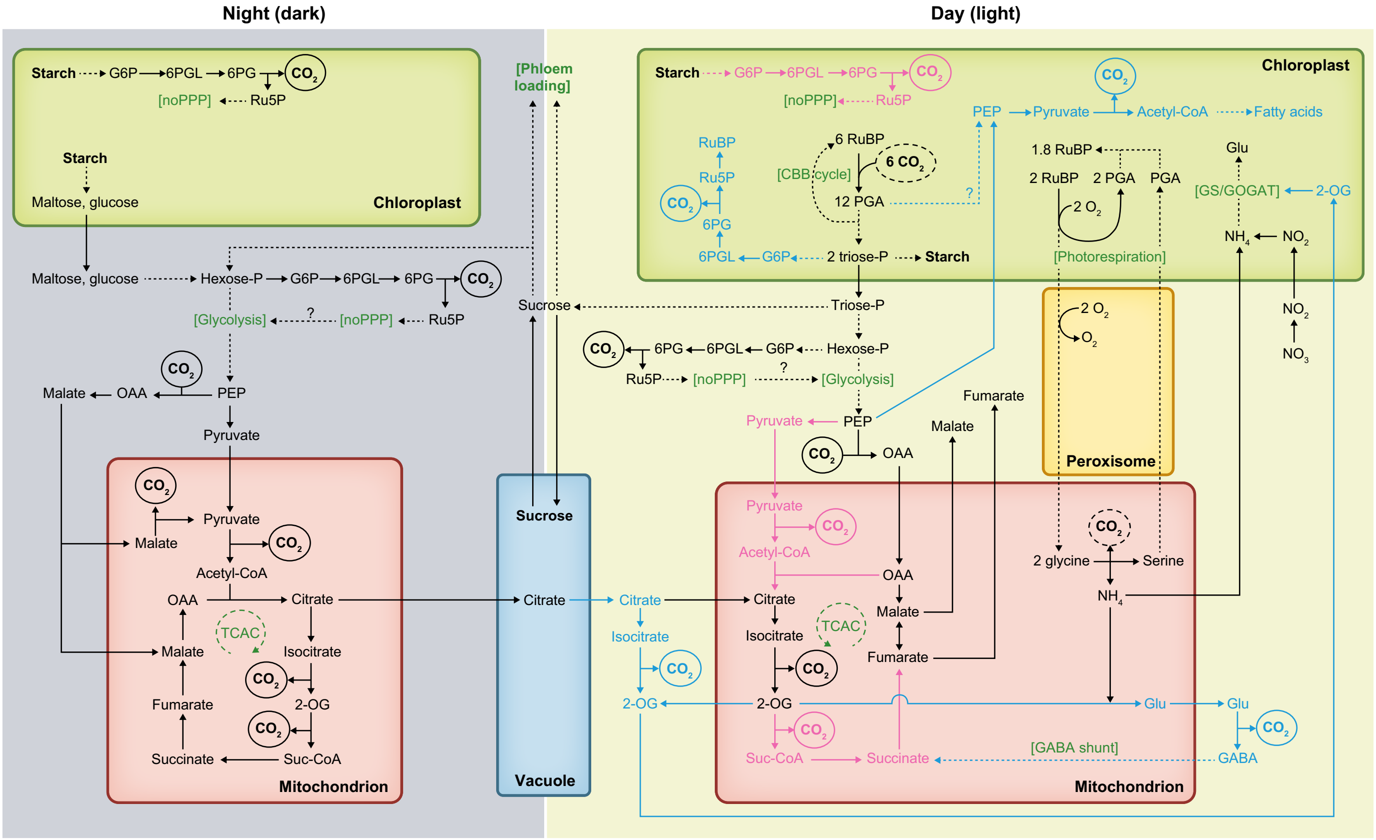

Fig. 3 Major metabolic reactions associated with mature-leaf respiratory CO_2 release at night (left) and during the day (right). Solid lines indicate single enzyme (or enzyme complex) reactions or intracellular transport. Dashed lines indicate multi-enzyme sequences. Major pathways without all intermediate reactions shown are indicated by green text in brackets (e.g. [glycolysis]). This scheme does not show ATP formation or $NAD(P)^+/NAD(P)H$ interconversion. CO_2 exchanges associated with respiration, including CO_2 (in the form HCO_3^-) assimilation during conversion of PEP to OAA, are circled with solid lines. CO_2 exchanges associated with photosynthesis, that is the CBB cycle, and photorespiration are circled with dashed lines. On the right, respiration-related reactions and pathways that may be slowed or halted in the light are shown in pink while CO_2-releasing reactions and pathways that may be stimulated by light or photosynthesis are shown in blue. 2-OG, 2-oxoglutarate; 6PG, 6-phosphogluconate; 6PGL, 6-phosphogluconolactone; CBB, Calvin-Benson-Bassham; G6P, glucose 6-phosphate; GABA, γ-aminobutyric acid; Glu, glutamate; GS/GOGAT, glutamine synthetase/glutamine oxoglutarate aminotransferase; noPPP, nonoxidative reactions of the pentose phosphate pathway; OAA, oxaloacetate; PEP, phospho*enol*pyruvate; PGA, 3-phosphoglycerate; Ru5P, ribulose 5-phosphate; RuBP, ribulose 1,5-bisphosphate; suc-CoA, succinyl-CoA; TCAC, tricarboxylic acid cycle; triose-P, triose phosphate. Further explanation of this figure can be found in Supporting Information Notes S4.

released in chloroplasts can be more readily refixed by Rubisco than CO_2 released in mitochondria and cytosol. Also, daytime 2-oxoglutarate use in support of glutamate production in chloroplasts for photorespiratory-NH_4 recovery (along with general NO_3 assimilation) may account for increased light inhibition of respiration with increasing photorespiration (Fig. 3). Perhaps more importantly, the chloroplast-localized oxidative pentose phosphate pathway (PPP) not only carries an anaplerotic carbon flux into, but provides NADPH (thus electrons) to, the Calvin–Benson–Bassham cycle (Wieloch, 2022).

To account for effective electron supply changes from the usual J to $(J+4R_{a,p})$, where $R_{a,p}$ is CO_2-release rate by chloroplastic oxidative PPP, Wieloch *et al.* (2023) revised Eqn 1 to:

$$A=\frac{(C_c-\Gamma_*)(J+4R_{a,p})}{4(C_c+2\Gamma_*)}-R_{a,p}-R_x \qquad \text{Eqn 4}$$

where R_x is day respiration other than $R_{a,p}$, including all other daytime respiratory components of Fig. 3 (i.e. $R_{a,p}+R_x=R_d$).

If $R_{a,p}$ is a significant fraction of R_d, current R_d-estimating methods should be re-assessed. Eqn 4 indicates that $R_{a,p}$ alters slopes of curves in the Laisk plot, but if $R_{a,p}$ does not vary with CO_2 or I_{inc} (see cautions later), the common intercept of the Laisk plot still gives an estimate of $-(R_{a,p}+R_x)$, that is $-R_d$, although $R_{a,p}$ and R_x cannot be separated in this method.

Rewriting Eqn 4 as:

$$A=\frac{(C_c-\Gamma_*)}{(C_c+2\Gamma_*)}\frac{J}{4}-\left[\left(1-\frac{C_c-\Gamma_*}{C_c+2\Gamma_*}\right)R_{a,p}+R_x\right] \qquad \text{Eqn 5}$$

indicates that the intercepts of neither the Kok plot nor the Yin plot are $-(R_{a,p}+R_x)$, and one can hardly use these methods to estimate R_d. Nonetheless, for nonphotorespiratory conditions (e.g. 2% O_2), where $(C_c-\Gamma_*)/(C_c+2\Gamma_*)$ approaches unity, Eqn 5 becomes: $A=J/4-R_x$, and then the Kok and Yin methods can be applied, but the intercept estimate $-R_x$.

For the NRH-A method, Eqn 3 is applicable if x_1 is changed from $J/4$ to $(J+4R_{a,p})/4$ and R_d is changed to $(R_{a,p}+R_x)$. As R_d is then split into $R_{a,p}$ and R_x, overfitting may occur, but if R_x is simultaneously estimated from the Yin method applied to a nonphotorespiratory condition (as mentioned in the previous paragraph), then $R_{a,p}$ can be estimated by the NRH-A method. This assumes that photorespiration does not affect R_x or $R_{a,p}$. If $R_{a,p}$ relative to R_x varies with CO_2 level (Wieloch, 2022) or with other factors like I_{inc} (light may alter the chloroplastic oxidative PPP), it will be difficult to estimate them from conventional gas exchange measurements.

VI. Conclusions

Adding chlorophyll fluorescence measurements to gas exchange data improves the estimation of R_d. Variation in R_d estimates can be due to: (1) photorespiratory vs nonphotorespiratory conditions, (2) reassimilation of respired CO_2, and (3) assumptions behind the methods. When methods are appropriately applied (i.e. the NRH-A method applied to photorespiratory conditions and the Yin method to nonphotorespiratory conditions), different results will likely reflect real differences in R_d between the two measurement conditions. Underestimation of R_d with the Yin method applied to photorespiratory conditions, relative to the NRH-A method, should reflect reassimilation of respired CO_2. As the Laisk method intrinsically relies on highly photorespiratory measurement conditions, it is inappropriate for estimating R_d in C_4 species (Yin *et al.*, 2011) or in C_3 species in low-photorespiration situations, for example low temperatures (Way *et al.*, 2019). Underestimations of R_d by the Laisk method, relative to the NRH-A method, can be due to underestimation of reassimilation of respired CO_2. The Kok method underestimates R_d to the greatest extent, because it ignores both the Φ_2 decline with increasing I_{inc} and CO_2 reassimilation.

The potentially diverse metabolic origins of R_d (Fig. 3) indicate: (1) R_d may be dominated by nonmitochondrial processes (and see Wieloch, 2022) and ‘mitochondrial respiration in the light’ should be avoided as an alternative name for day respiration; (2) while some key respiratory reactions can be suppressed by light, others may be stimulated; (3) daytime 2-oxoglutarate use in support of photorespiratory-NH_4 recovery and general NO_3 assimilation, which might reduce mitochondrial CO_2 release, may be a major factor underlying light inhibition of respiration in general and especially with increasing photorespiration; and (4) Eqn 1 implies that R_d and photosynthesis are independent, but they are interdependent and R_d must be partitioned into different components if the chloroplast-based oxidative PPP accounts for a significant part of R_d. Further research should identify: contributions of various CO_2-exchange processes to R_d, variation in those contributions between species and environments/conditions, the CO_2-exchange processes most often inhibited *or stimulated* by light, and whether R_d is affected differentially in low- and high-light conditions.

Competing interests

None declared.

Author contributions

XY and JSA conceived, wrote, and revised the article.

ORCID

Jeffrey S. Amthor https://orcid.org/0000-0001-8601-403X
Xinyou Yin https://orcid.org/0000-0001-8273-8022

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Illustration of the (under)estimation of R_d for photorespiratory conditions.

Methods S1 SAS script for the Laisk method that ensures a common intersection point.

Methods S2 R script for the Laisk method that ensures a common intersection point.

Methods S3 SAS script for the NRH-A method to simultaneously estimate R_d and g_m.

Methods S4 R script for the NRH-A method to simultaneously estimate R_d and g_m.

Notes S1 Full caption text of Fig. 1.

Notes S2 Full caption text of Fig. 2.

Notes S3 Refixation fractions of (photo)respired CO_2 in relation to resistance components.

Notes S4 Full caption text of Fig. 3.