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# Simple and Accurate Representation of Cumulative Nighttime Leaf Respiratory $CO_2$ Efflux

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### ABSTRACT

Leaf respiratory carbon loss decreases independent of temperature as the night progresses. Detailed nighttime measurements needed to quantify cumulative respiratory carbon loss at night are challenging under both lab and field conditions. We provide a simple yet accurate approach to represent variation in nighttime temperature-independent leaf respiratory $CO_2$ efflux in environments with both stable and fluctuating temperatures, which requires no detailed measurements throughout the night. We demonstrate that the inter- and intraspecific variation in the cumulative leaf respiratory $CO_2$ efflux at constant temperature, at any length of night, scales linearly with the inter- and intraspecific variation in initial measurement of leaf respiratory $CO_2$ efflux at the same temperature at the beginning of the night. This approach informs large-scale predictions of cumulative leaf respiratory $CO_2$ efflux, which is needed to understand plant carbon economy in global change studies as well as in global modeling and eddy covariance monitoring of the land–atmosphere exchange of $CO_2$.

## 1 | Introduction

Plant respiration provides the necessary energy and carbon skeletons for cellular growth and maintenance and at the same time releases $CO_2$ as a byproduct from decarboxylation (Lambers, Chapin, and Pons 2008). Leaf respiratory $CO_2$ efflux ($R_{CO_2}$) constitutes an important proportion of plant carbon loss to the atmosphere for all levels from individuals (Lavigne et al. 1997; Amthor and Baldocchi 2001; Atkin, Scheurwater, and Pons 2007; Malhi, Doughty, and Galbraith 2011) to global level (Amthor and Baldocchi 2001; Malhi et al. 2009; Atkin et al. 2017; Bruhn et al. 2022). Here, we focus on nighttime variation of leaf $R_{CO_2}$, which plays a critical role in understanding plant functioning because this respiratory carbon loss is temporarily isolated from daytime carbon uptake. However, variation in $R_{CO_2}$ remains a major knowledge gap

in terms of its drivers and how it is quantified by the empirical and vegetation modeling communities (Bruhn et al. 2022; Bruhn, Povlsen, et al. 2024). This is at least in part because monitoring variation in nighttime leaf $R_{CO_2}$ via high temporal resolution non-automated measurements is inherently challenging under stable temperature environments, for example, in growth cabinets, but in particular under fluctuating temperature environments, for example, in remote and difficult to reach field sites. Therefore, the development of a simple, yet accurate representation of variation in nighttime $R_{CO_2}$ is critical for future attempts to engineer plant respiration to enhance crop yield (Amthor et al. 2019; Garcia et al. 2023), future studies of how the components of plant net carbon budgets respond to climate change (Shapiro et al. 2004; Atkin, Bruhn, Hurry, et al. 2005; Atkin, Bruhn, and Tjoelker 2005; Hartley et al. 2006; Ayub et al. 2011; Hüve et al. 2012; Noguchi

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et al. 2015; Rasulov et al. 2015; Ikkonen et al. 2020; Dewhirst et al. 2021), future terrestrial biosphere models (TBMs; Clark et al. 2011; Reick et al. 2021) and earth system models (ESMs; Jones and Friedlingstein 2020), and for accurate estimation of ecosystem respiration from eddy covariance (Lavigne et al. 1997).

The assumption of full temperature control of variation in $R_{CO_2}$ on a diel timescale has for a long time been pivotal to the understanding of temporal variation in leaf $R_{CO_2}$ (cf. Bruhn et al. 2022 for a discussion), and thus, much research and modeling has focussed on how to represent the temperature sensitivity of leaf $R_{CO_2}$ (cf. Bruhn 2024; Bruhn, Povlsen, et al. 2024 for a discussion) and a "base" $R_{CO_2}$ at constant temperature ($R_{CO_2,T_o}$). Using this "base" $R_{CO_2}$, inter- and intraspecific variation in nighttime $R_{CO_2,T_o}$ has traditionally been predicted from correlations between $R_{CO_2,T_o}$ and various leaf traits (Reich et al. 2006; Wright et al. 2006; Atkin et al. 2015; Slot et al. 2014), both of which typically are measured at an unknown time during daytime (Reich et al. 2006; Wright et al. 2006; Atkin et al. 2015). However, it was recently demonstrated that leaf $R_{CO_2,T_o}$ is not a constant at the diel scale (Amthor, Koch, and Bloom 1992; Bruhn et al. 2008; Bruhn 2023; Bruhn et al. 2022; Bruhn, Povlsen, et al. 2024; Bruhn, Noguchi, et al. 2024; Faber et al. 2022). Indeed, $R_{CO_2,T_o}$ systematically decreases during nighttime (Amthor, Koch, and Bloom 1992; Bruhn 2023; Bruhn et al. 2022; Bruhn, Povlsen, et al. 2024; Bruhn, Noguchi, et al. 2024; see also Figure 1a), which fundamentally challenges an accurate representation of inter- and intraspecific variation of nighttime leaf $R_{CO_2}$. The classical method should thus no longer be used in its present form.

Here, we test how well inter- and intraspecific variation in cumulative $R_{CO_2,T_o}$ over a night ($\Sigma R_{CO_2,T_o}$, see Figure 1a) scale with inter- and intraspecific variation in $R_{CO_2,T_o}$ measured at the beginning of the night. If these two variables are strongly correlated, then future inter- and intraspecific variation in $\Sigma R_{CO_2,T_o}$ over any given length of nighttime could be accurately represented via leaf traits (Reich et al. 2006; Wright et al. 2006;

Atkin et al. 2015; Figure S1) that can easily be measured during daytime. The earlier assumption of full temperature control of $R_{CO_2}$ on a diel timescale logically predicts that the $\Sigma R_{CO_2,T_o}$ for a given length of night will depend directly on $R_{CO_2,T_o}$ measured at the beginning of the night in a linear fashion with length of the night. However, the $\Sigma R_{CO_2,T_o}$ for a given length of night will depend on both $R_{CO_2,T_o}$ measured at the beginning of the night as well as on the decay rate of the nocturnal decrease in leaf $R_{CO_2,T_o}$ (see Figure 1a). Also, inter- and intraspecific variation in $R_{CO_2,T_o}$ measured at the beginning of the night and in the decay rate of the nocturnal decrease in leaf $R_{CO_2,T_o}$ is not well examined. That is why even though we expect a positive relationship between $\Sigma R_{CO_2,T_o}$ and $R_{CO_2,T_o}$ measured at the beginning of the night, we still do not know (i) what the slope might be, (ii) the strength of the relationship, and (iii) whether there is a linear or perhaps nonlinear relationship between these variables.

## 2 | Material and Methods

### 2.1 | Data

Data for $R_{CO_2,T_o}$ from 14 different species from trees and herbaceous tropical and temperate systems from Bruhn et al. (2022) were used in this study (see Bruhn, Slot, and Mercado 2024, https://doi.org/10.5281/zenodo.13850860 and Tables S1 and S2).

In the field (United Kingdom, Denmark, Panama, Colombia and Brazil), $R_{CO_2,T_o}$ ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$) was measured through nocturnal periods at $T_o$ (controlled either by the target leaf temperature or the block temperature of the cuvette) with infrared gas analyzers (LiCor-6400(XT) or LiCor-6800, Lincoln, Nebraska, USA). Mature, attached leaves positioned in the sunlight throughout the day were chosen. Target [$CO_2$] in the leaf cuvette was set to ambient, ranging from 390 to 410 ppm, depending on when measurements were made, and target RH = 65% ± 10%, with a flow rate of 300 $\mu mol\,s^{-1}$. The $R_{CO_2,T_o\text{-beginning of night}}$ was defined as $R_{CO_2,T_o}$ at first measurement after darkness 30 min
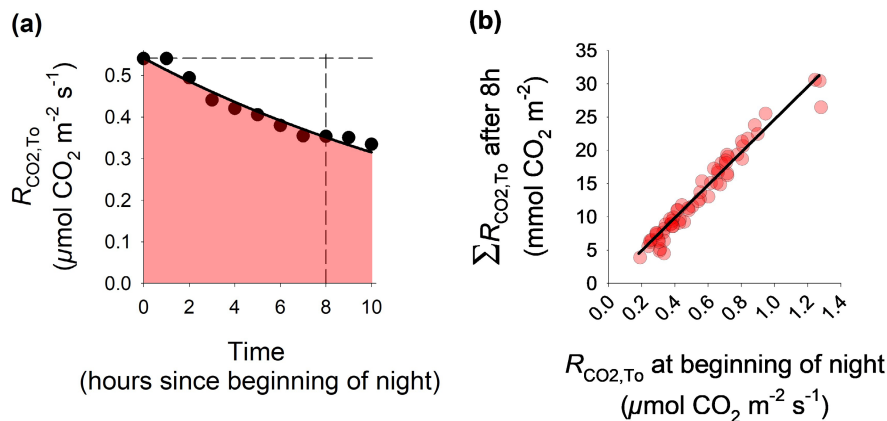


**FIGURE 1** | Illustration of nighttime decrease in leaf $R_{CO_2,T_o}$ and inter- and intraspecific relationships between nighttime $\Sigma R_{CO_2,T_o}$ and $R_{CO_2,T_o}$ at beginning of night. (a) Example of the nighttime decrease in leaf $R_{CO_2,T_o}$ (Bruhn et al. 2022) in one replicate specimen of *Forsythia* over the course of a night (filled circles). An exponential decay regression was fitted: Leaf $R_{CO_2,T_o} = a \times e^{(-b \times h)}$, where $a$ is $R_{CO_2,T_o}$ at beginning of the night and $b$ is the decay rate. The area under the regression line (coloured red) is the cumulative $R_{CO_2,T_o}$, that is, $\Sigma R_{CO_2,T_o}$. The horizontal dashed line represents $R_{CO_2}$ if it was only controlled by temperature, as it is typically assumed. Regression details for all specimens within the 14 tested species are given in Table S2. (b) Inter- and intraspecific relationship between $\Sigma R_{CO_2,T_o}$ for an 8-h night and $R_{CO_2,T_o}$ at beginning of the night across 14 species (red symbols). Linear regression: $\Sigma R_{CO_2,T_o}$ for an 8-h night = $5.3209 \times R_{CO_2,T_o}$ at beginning of the night ($R^2 = 0.97$; $p < 0.0001$ for the slope).

after sunset (to conservatively avoid light-enhanced dark respiration) (Azcón-Bieto and Osmond 1983; Atkin, Evans, and Siebke 1998). Leak tests were conducted prior to measurements (Bruhn, Mikkelsen, and Atkin 2002). The temporal resolution of measurements varied between every 3 min to once per hour for the different species without direct effects of stomatal conductance on leaf $R_{CO_2}$ measurements (Bruhn, Faber, et al. 2024). Data were subsequently binned in hourly bins (Bruhn et al. 2022).

## 2.2 | Data Analysis

For each combination of species, replicate specimen leaf and night, an exponential decay regression was fitted to $R_{CO_2,T_o}$ as a function time (hours since onset of darkness, $h$, see also Figure 1a for an example) during the night at set $T_o$, $R_{CO_2,T_o} = a \times e^{(-b \times h)}$, where $a$ is the $R_{CO_2,T_o,\text{beginning of night}}$ and $b$ is the decay rate of the nocturnal decrease in leaf $R_{CO_2,T_o}$ using the regression software in SigmaPlot 14.5. The resulting regression coefficients are shown in Table S1. Five out of the total of 65 tested leaves exhibited a statistically nonsignificant $b$ coefficient, so these five replicates were omitted in further analysis. Cumulative $R_{CO_2,T_o}$, $\Sigma R_{CO_2,T_o}$, for any length of night (Figure 1b; Figure S2), was calculated by integration of the above exponential decay regressions.

## 3 | Results and Discussion

### 3.1 | Relationship Between Initial Measurement and Cumulative Nighttime Leaf Respiratory CO$_2$ Efflux

Our results (Figure 1b) demonstrate that the inter- and intraspecific variation in cumulative $R_{CO_2,T_o}$, $\Sigma R_{CO_2,T_o}$, scales linearly with the inter- and intraspecific variation in $R_{CO_2,T_o}$, at the beginning of the night (i.e., $R_{CO_2,T_o,\text{beginning of night}}$) (Figure 1b), at any length of night (Figure S2). Also, the decay rate (Figure 1a) is independent of $R_{CO_2,T_o,\text{beginning of night}}$ both among (Figure S3) and within species (Figure S4).

### 3.2 | Modeling Cumulative Nighttime Leaf Respiratory CO$_2$ Efflux

Many empirical studies are conducted in growth cabinets under stable temperature environments (Shapiro et al. 2004; Hartley et al. 2006; Ayub et al. 2011; Hüve et al. 2012; Noguchi et al. 2015; Rasulov et al. 2015; Ikkonen et al. 2020; Dewhirst et al. 2021) and although $R_{CO_2,T_o}$ decreases nonlinearly during nighttime (Amthor, Koch, and Bloom 1992; Bruhn 2023; Bruhn et al. 2022; Bruhn, Povlsen, et al. 2024; Bruhn, Noguchi, et al. 2024) (see Figure 1a; Table S2), in such studies, inter- and intraspecific variation in $\Sigma R_{CO_2,T_o}$ (in mmol CO$_2$ m$^{-2}$) can now very easily be predicted as (see Figure S2):

$$\Sigma R_{CO_2,T_o} \times h \left( \text{mmol CO}_2 \text{ m}^{-2} \right) = \left( -0.059 \times h^2 + 3.55 \times h \right) \times \left( 3.6 \text{ mmol } \mu\text{mol}^{-1} \text{ s h}^{-1} \right) \times R_{CO_2,T_o,\text{beginning-of-night}} \left( \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \right)$$

(1)

In empirical (Lavigne et al. 1997) and modeling (Bruhn et al. 2022; Clark et al. 2011; Jones and Friedlingstein 2020) studies, it is typically necessary to consider not only the length of the night but also a fluctuating temperature during nighttime. Bruhn et al. (2022) suggested to model nighttime variation in leaf $R_{CO_2}$ in response to both time ($t$) of night and temperature ($T$) with a globally applicable equation derived from temperate and tropical species:

$$R_{CO_2,T,t} = R_{CO_2,T_o,\text{beginning-of-night}} \times Q_{10}^{0.1 \times (T,t-T,\text{beginning-of-night})} \times \left( 1 - 0.08 \times h^{0.54} \right)$$

(2)

where $h$ is hours since the beginning of the night. However, the validity of Bruhn et al. (2022) in terms of inter- and intraspecific variation in leaf $R_{CO_2,T_o}$ remained unclear. The analysis presented here (Figures S3 and S4) demonstrates that the equation from Bruhn et al. (2022) (Equation 2) can accurately represent both inter- and intraspecific variation in leaf $R_{CO_2}$ in response to both time of night and temperature. The next logical step needed to quantify the variation of nocturnal leaf respiration (Figure S1) is the prediction of $R_{CO_2,T_o}$ at the beginning of the night from easy to measure leaf traits.

### 3.3 | Timing of Measurements of Leaf Respiratory CO$_2$ Efflux

Large-scale predictions of $\Sigma R_{CO_2,T_o}$ across multiple species and conditions would be possible in future studies under both stable and fluctuating temperature environments (Figure S1) if the timing is standardized for the $R_{CO_2,T_o}$ measurements to be correlated with leaf traits. While leaf traits are typically rather stable over short timespans (O'Leary et al. 2017), both leaf $R_{CO_2,T_o}$ (Bruhn, Povlsen, et al. 2024) and the temperature sensitivity of $R_{CO_2}$ (Bruhn, Povlsen, et al. 2024) can differ between nighttime and "dark-acclimated" daytime measurements; we therefore strongly encourage that future work toward understanding of the potential relationship between leaf traits and $R_{CO_2,T_o}$ at the beginning of the night (Figure S1) is done using data collected at the beginning of the night, avoiding end-of night and daytime $R_{CO_2,T_o}$ measurements (Bruhn 2023; Bruhn et al. 2022; Bruhn, Povlsen, et al. 2024; Bruhn, Noguchi, et al. 2024; Faber et al. 2022). This future relationship per se may further be affected by, for example, environmental effects on photosynthesis the previous day.

### 3.4 | Causes for Variation in Leaf Respiratory CO$_2$ Efflux

$R^2$ of the linear relationship in Figure 1b is surprisingly high ($R^2 = 0.97$), as it is a combination of both inter- and intraspecific variation (see Figure S5). The variation in $R_{CO_2,T_o}$ at the beginning of the night shown in Figure 1b ($x$-axis) is likely associated with differences in one or more of the commonly measured leaf traits (e.g., leaf mass per area (LMA) and leaf [N]), which serve as proxies for leaf economic strategy and the associated energy demand (typically indicated by respiratory O$_2$-uptake, $R_{O_2}$). Leaf energy demand reflects the level of ATP requiring processes (Fondy and Geiger 1982; Hendrix and Huber 1986; Noguchi and Terashima 1997; Grimmer and

Komor 1999; Matt et al. 2001) and may be modified by relative engagement of the alternative oxidase (Svensson and Rasmusson 2001; Dutilleul et al. 2003). Variation in $R_{CO_2, T_o}$ at the beginning of the night in Figure 1b may also be associated with differences in the amount of respiratory substrates (Fondy and Geiger 1982; Azcón-Bieto and Osmond 1983; Hendrix and Huber 1986; Grimmer and Komor 1999; Hüve et al. 2012; Jones et al. 2024), rates of phloem loading (Grimmer and Komor 1999), and variation in the respiratory quotient (molar ratio of respiratory $CO_2$ efflux to $O_2$ uptake; Bruhn, Noguchi, et al. 2024; Fan et al. 2024). All of these variables are also likely to cause the variation in $\Sigma R_{CO_2, T_o}$ ($y$-axis) in Figure 1b. It is still unknown to what extent each of the above-mentioned causes to variation in leaf respiratory $CO_2$ efflux affects inter- and intraspecific variation in $R_{CO_2, T_o}$ at the beginning of the night, and in the decay rate of the nocturnal decrease in leaf $R_{CO_2, T_o}$, and hence $\Sigma R_{CO_2, T_o}$. The fact that the slope of the interspecific linear relationship (Figure S5a) is lower than the intraspecific linear relationship (Figure S5b) suggests that whatever the mechanism(s) underlying intraspecific variation in leaf respiratory $CO_2$ efflux differs from an interspecific variation. This suggests that, in future studies, effects of, for example, ontogeny and environment may be detected in analyses as in Figure S5b.

Although we found large variability (Table S2) in both the $a$ coefficient (0.1817–1.2699 μmol $CO_2$ m$^{-2}$ s$^{-1}$) and the $b$ coefficient (0.0101–0.2158; $p < 0.05$) of the fitted exponential decay regressions, we found no inter- or intraspecific systematic variation between the $a$ and the $b$ coefficients (Figures S3 and S4). The relationship proposed in this technical advance of leaf $\Sigma R_{CO_2, T_o}$ at leaf level (Figure 1b) is ideal for implementation at ecosystem level and larger scale due to its simplicity. Any systematic correlation between these coefficients $a$ and $b$ (Figures S3 and S4) could introduce far more complex relationships (Figure S6) that would be challenging to implement in large-scale vegetation modeling and growth cabinet experiments.

## 3.5 | Implications for Carbon Economy Estimates

Nocturnal ecosystem respiratory $CO_2$ efflux can, for example, in boreal sites, release 30%–100% of the $CO_2$ fixed during daytime photosynthesis, of which nocturnal leaf $R_{CO_2}$ is assumed to constitute 25%–43% (Lavigne et al. 1997). The slope of the linear relationship in Figure 1b for an example of an 8-h night is $100 \times (8 - 5.3209)/8 = 33\%$ less than the earlier assumption of full temperature control of $R_{CO_2}$ on a diel timescale. Thus, in addition to providing simple estimates of integrals of leaf $R_{CO_2}$ over any interval of time, we can already establish that thus far, we have likely overestimated nocturnal leaf $R_{CO_2}$ greatly. This suggests that the contribution of stem- and root + soil $R_{CO_2}$ would be relatively higher than hitherto assumed (Lavigne et al. 1997).

The findings presented here regarding nocturnal variation of leaf $R_{CO_2, T_o}$ (Figure 1; Figure S5) are, therefore, pivotal to disciplines that estimate the integrals of $R_{CO_2}$ over any interval of time, that is, scaling of components of autotrophic respiration at plant (i.e., leaf, stem and root), and ecosystem level for the estimation of net and gross primary productivity using biometric

methods and eddy covariance, estimation of ecosystem respiration and gap filling in eddy covariance studies (Falge et al. 2001), and TBMs (Clark et al. 2011; Reick et al. 2021) and ESMs (Jones and Friedlingstein 2020) in which nighttime variation in $R_{CO_2}$ of components other than leaf is based on nighttime variation in leaf $R_{CO_2}$ (Clark et al. 2011). Furthermore, this study offers a simple method to predict $R_{CO_2, T_o}$ integrated over any length of night under field conditions in the absence of leaf temperature measurements during respiration.

As the slope of the linear relationship in Figure 1b is a mix of both inter- and intraspecific variation, it suggest that representing leaf $\Sigma R_{CO_2, T_o}$ of a terrestrial ecosystem would not require a strict sampling regime of measurements of $R_{CO_2, T_o}$ at the beginning of the night with a rigorous focus on an exact balanced number of intraspecific replicates across the measured species.

The principal underlying this technical advance was derived from a dataset consisting primarily of tropical species (Table S1). Therefore, it remains to be tested whether the slopes in Figure 1b and Figure S2a would be different in temperate and boreal regions, where the regression coefficients "$a$" and "$b$" might be affected by seasonal changes in daylength, environmental parameters, and phenology.

**Conflicts of Interest**

The authors declare no conflicts of interest.

**Data Availability Statement**

Data underlying figures are all available from the 'Nocturnal leaf respiratory $CO_2$ release in different species measured at constant temperature'. Zenodo [Dataset]. https://doi.org/10.5281/zenodo.13850860.

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**Supporting Information**

Additional supporting information can be found online in the Supporting Information section.