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Viewpoint

Instantaneous Q_{10} of night-time leaf respiratory CO_2 efflux – measurement and analytical protocol considerations

Summary

The temperature sensitivity (e.g. Q_{10}) of night-time leaf respiratory CO_2 efflux (R_{CO_2}) is a fundamental aspect of leaf physiology. The Q_{10} typically exhibits a dependence on measurement temperature, and it is speculated that this is due to temperature-dependent shifts in the relative control of leaf R_{CO_2} . Two decades ago, a review hypothesized that this mechanistically caused change in values of Q_{10} is predictable across plant taxa and biomes. Here, we discuss the most appropriate measuring protocol among existing data and for future data collection, to form the foundation for a future mechanistic understanding of Q_{10} of leaf R_{CO_2} at different temperature ranges. We do this primarily via a review of existing literature on Q_{10} of night-time R_{CO_2} and only supplement to a lesser degree with own original data. Based on mechanistic considerations, we encourage that instantaneous Q_{10} of leaf R_{CO_2} to represent night-time should be measured: only at night-time; only in response to short-term narrow temperature variation (e.g. max. 10°C) to represent a given midpoint temperature at a time; in response to as many temperatures as possible within the chosen temperature range; and on still attached leaves.

Temperature (T) controls *c.* half of the temporal variation in leaf respiratory CO_2 efflux (R_{CO_2}) during the night (Bruhn *et al.*, 2022) due to a T sensitivity of R_{CO_2} , for example Q_{10} (i.e. the proportional change in R_{CO_2} measured 10°C apart). Q_{10} is the most common expression of T sensitivity of leaf R_{CO_2} (Supporting Information Fig. S1), and it is used both in modelling of night-time plant R_{CO_2} along temporal- and spatial scales (Clark *et al.*, 2011) and in T-standardizing R_{CO_2} measured at different T to examine the effect of other variables, such as for example leaf [N] and species (Reich *et al.*, 2006; Wright *et al.*, 2006; Atkin *et al.*, 2015). Therefore, it is important that we achieve a good understanding of the values of Q_{10} . Q_{10} of leaf R_{CO_2} often appears to be dependent on the measurement of T *per se* (Wager, 1941; Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003; Atkin *et al.*, 2005a, b; Heskel *et al.*, 2016), and it has been hypothesized that the relative control of the different underlying physiological, biochemical, and

physical mechanisms of Q_{10} of leaf R_{CO_2} may change at different T ranges (Atkin & Tjoelker, 2003; Kruse *et al.*, 2008). To enhance our understanding of the ‘dynamic response of plant respiration to T’ (Atkin & Tjoelker, 2003) in terms of leaf R_{CO_2} , and how the relative control of the different underlying physiological, biochemical, and physical mechanisms of Q_{10} of leaf R_{CO_2} may change at different T ranges (Atkin & Tjoelker, 2003; Kruse *et al.*, 2008), we consider that it is important to separate the T effect from other dynamic changes in factors that may affect leaf R_{CO_2} .

In this viewpoint paper, we put forward some protocol considerations regarding the measuring of the short-term Q_{10} of night-time leaf R_{CO_2} . Thus, here we discuss the selection of existing data and considerations of future data collection to be used in a general $Q_{10}(\text{T})$ -relationship of night-time leaf R_{CO_2} , which can form the foundation for future mechanistic understanding of Q_{10} at different T ranges (Atkin & Tjoelker, 2003; Kruse *et al.*, 2008). We do this primarily via a review of existing literature on Q_{10} of night-time R_{CO_2} and only supplement to a lesser degree with own original data.

Daytime ‘dark’ (i.e. nonphotorespiratory) leaf R_{CO_2} appears to be inhibited by light (Atkin *et al.*, 2000a, b; Buckley & Adams, 2011; Tcherkez *et al.*, 2017a, b), and it has been thoroughly discussed (Villar *et al.*, 1994; Peisker & Apel, 2001; Yin *et al.*, 2011; Tcherkez *et al.*, 2017a, b; Berghuijs *et al.*, 2019; Yin & Amthor, 2024) that daytime leaf R_{CO_2} must be estimated via indirect techniques in the light (e.g. Kok, 1948; Laik, 1977; Haupt-Herting *et al.*, 2001; Yin *et al.*, 2011; Berghuijs *et al.*, 2019). The Q_{10} of daytime light-inhibited leaf R_{CO_2} is thoroughly discussed elsewhere (Atkin *et al.*, 2005b; Way *et al.*, 2019; Zheng *et al.*, 2024), therefore, in the present viewpoint, we focus only on night-time measurements of Q_{10} of leaf R_{CO_2} .

Q_{10} of night-time leaf R_{CO_2} must be measured at night

In a comprehensive review of the dynamic response of plant respiration to T, Atkin & Tjoelker (2003) proposed that the main mechanistic reasons underlying a T-mediated change in values of Q_{10} to be a gradual change in the relative control of R shifting from the maximum capacity of respiratory enzymes (i.e. enzymes in the glycolysis, tricarboxylic acid cycle, and mitochondrial electron transport) at lower temperatures towards the limitation of R at higher temperatures mainly via the availability of respiratory substrates and/or the use of respiratory products, for example ATP. Both Wager (1941) and Atkin & Tjoelker (2003) have speculated that values of Q_{10} scale positively with the level of respiratory substrates. We interpret this supposed mechanism (Atkin & Tjoelker, 2003) of varying Q_{10} with measurement T (Wager, 1941; Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003; Atkin *et al.*, 2005a, b; Heskel *et al.*, 2016) as control of R at a given T, which change in relative importance at different T ranges. Therefore, timing of

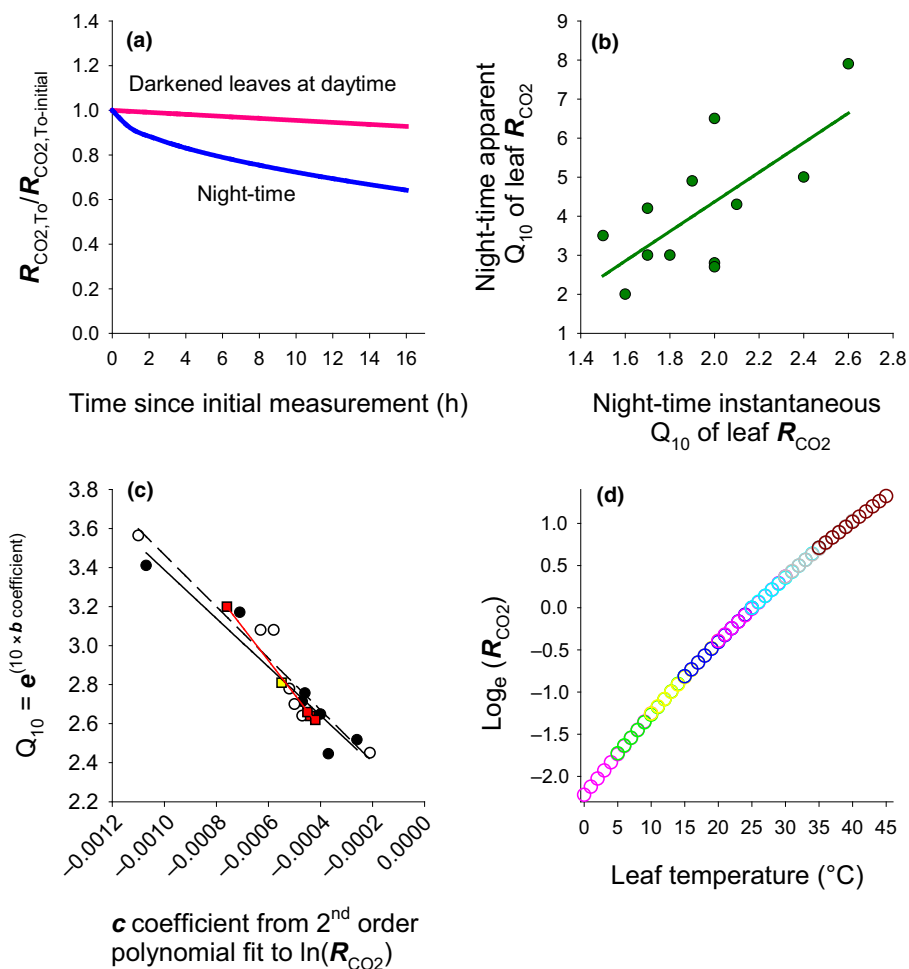


Fig. 1 Analytical considerations for estimation of Q_{10} of night-time leaf R_{CO_2} . (a) average temporal development in leaf R_{CO_2} measured at constant temperature (T_0) in relation to the initial measurement of either daytime (red line; based on 17 field-grown species in Faber *et al.*, 2022) or night-time (blue line; based on 31 field- and laboratory-grown species in Bruhn *et al.*, 2022). (b) relationship between apparent Q_{10} and instantaneous Q_{10} of night-time leaf R_{CO_2} in 10 different species (some measured at different times of year) from Bruhn *et al.* (2022). (c) Collinearity between the c coefficients and calculated Q_{10} at 0°C as $e^{(10 \times b \text{ coefficient})}$ from $\ln(R_{CO_2}) = a + bT + cT^2$ fits from Heskell *et al.* (2016). Closed circles represent different biomes; linear regression $Q_{10} = 2.14 \pm 0.09$ (mean \pm SE, $P < 0.0001$) – 1245.41 ± 156.0 (mean \pm SE, $P = 0.0005$), $R^2 = 0.9272$, $n = 7$. Open circles represent different Plant Functional Types; linear regression $Q_{10} = 2.14 \pm 0.11$ (mean \pm SE, $P < 0.0001$) – 1327.57 ± 181.13 (mean \pm SE, $P = 0.0007$), $R^2 = 0.9148$, $n = 7$. Red circles represent different temperature ranges (from 'Table S2' in Heskell *et al.*, 2016); linear regression $Q_{10} = 1.89 \pm 0.01$ (mean \pm SE, $P < 0.0001$) – 1729.31 ± 27.68 (mean \pm SE, $P = 0.0003$), $R^2 = 0.9995$, $n = 4$. Yellow circle represents calculated Q_{10} at 0°C using the entire 10–45°C (from Table S2 in Heskell *et al.*, 2016). (d) Over large temperature (T) ranges Q_{10} can be approximated at several midpoint- T s by linear fits of $\ln(R_{CO_2})/T$ over smaller T ranges. In the shown example, linear fits for midpoint- T s, 5°C, 10°C, 15°C, 20°C, 25°C, 30°C, 35°C, and 40°C are shown with changing colours, using a datapoint range of $\pm 5^\circ\text{C}$ around each midpoint- T . By this approach, values of Q_{10} at for example lower T s are not influenced by mechanisms particular for higher T ranges.

measurements of Q_{10} becomes important because the underlying factors affecting R at a given T can differ between different times of the 24-h cycle.

During the day, leaves typically exhibit temporal variation in dark-acclimated leaf R_{CO_2} at a set temperature (Faber *et al.*, 2022) that differs from that typically observed at night-time (Bruhn *et al.*, 2022; see Fig. 1a) and this may to some extent be caused by circadian rhythms in leaf R *per se* (Gessler *et al.*, 2017). However, in relation to the above-proposed mechanism of the dynamic response of plant respiration to T (Atkin & Tjoelker, 2003), it is also likely to be explained by temporal changes in substrate availability (Fondy & Geiger, 1982; Azcón-Bieto & Osmon, 1983; Noguchi &

Terashima, 1997; Grimmer & Komor, 1999; Flis *et al.*, 2019), rates of phloem loading (Grimmer & Komor, 1999), relative engagement of AOX:COX (Svensson & Rasmussen, 2001; Dutilleul *et al.*, 2003), and ATP requirements (Fondy & Geiger, 1982; Hendrix & Huber, 1986; Noguchi & Terashima, 1997; Grimmer & Komor, 1999; Matt *et al.*, 2001). In addition, because our focus here is on leaf R_{CO_2} rather than leaf respiratory oxygen uptake (R_{O_2}), it could also be explained to some degree by a temporal change in the respiratory quotient (ratio of CO_2 efflux to O_2 uptake; Bruhn *et al.*, 2024). Therefore, we consider it important to be careful with the interpretation of rates of daytime dark-acclimated leaf R_{CO_2} in general to represent night-time conditions relevant for leaf R_{CO_2} .

Most studies regarding Q_{10} of leaf R_{CO_2} have been conducted during the daytime on darkened leaves (Fig. S1). The above mechanistic considerations, however, suggest that for a value of Q_{10} to truly represent night-time conditions (e.g. availability of substrates and use of respiratory products) for R_{CO_2} in response to varying T, it is important that leaf R_{CO_2} is measured at night-time. In support of this, a recent study of eight plant species indicated that the calculated T sensitivity of dark-acclimated leaf R_{CO_2} can vary depending on the time of measurements through the 24-h cycle in different types of plants in environmentally controlled facilities (Qin *et al.*, 2024). We have here further added to this line of enquiry by examining values of Q_{10} of night-time leaf R_{CO_2} in another nine species grown and measured under naturally fluctuating conditions both early and late at night. We found that in two species (*Juglans ailanthifolia* Carr. and *Linnaea amabilis* Graebn. Christenh.) that Q_{10} of leaf R_{CO_2} appeared to differ between the different times of night. However, we did not find a general systematic statistically significant difference across all of the nine species between Q_{10} of night-time leaf R_{CO_2} at a given midpoint-T depending on whether measurements were done early or late at night, Welch two-sample *t*-test; $t = -0.66436$, $df = 12.765$, P -value = 0.5183 performed on $\ln(R_{CO_2})/T$ (Fig. S2).

A related concern is that in many published studies on Q_{10} of leaf R_{CO_2} , leaves or shoots were furthermore detached (e.g. predawn) and kept in darkness for hours before later measurements during daytime (Fig. S1). Amthor *et al.* (1992) have shown that night-time leaf R_{CO_2} at constant T can decrease even faster in the period exceeding 12 h of darkness compared with the decrease in the few hours just before 12 h of darkness. This suggests that such a methodological approach could result in the examination of values of Q_{10} of leaf R_{CO_2} for a given T range, where the underlying physiological conditions (e.g. availability of substrates and use of respiratory products) are not truly relevant (Kruse *et al.*, 2008) for the given T range.

Temperature manipulation of night-time leaf R_{CO_2} must be brief when studying instantaneous Q_{10}

The approach to studying the T-response for the calculation of a Q_{10} of night-time leaf R_{CO_2} is also important to consider. Bruhn *et al.* (2022) demonstrated a systematic difference between values of Q_{10} of night-time leaf R_{CO_2} obtained in response to short-term (minutes) T-manipulation of the leaf (i.e. instantaneous Q_{10}) and values of Q_{10} of night-time leaf R_{CO_2} obtained in response to longer-term natural T-variation of the environment experienced by the leaf over a period of hours (i.e. apparent Q_{10}). The values of apparent Q_{10} are higher than the values of the instantaneous Q_{10} (Fig. 1b). This is most likely explained by temporal variation in for example availability of respiratory substrates, rate of phloem loading, requirements for ATP, relative engagement of AOX: COX, and perhaps even the respiratory quotient (as described in the mechanistic discussion), which may cause leaf R_{CO_2} even at constant T to change through a period of hours during the night. Occasionally, an apparent Q_{10} is reported instead of instantaneous Q_{10} (Fig. S1), which we should be careful not to take as the representation of only the T effect *per se*. Rather, an apparent Q_{10} of night-time leaf R_{CO_2} for a given period represents a combination

of the instantaneous T sensitivity together with any change in leaf R_{CO_2} due to dynamic changes in factors other than T over the given period of measurements (Bruhn *et al.*, 2008, 2022, 2024; Bruhn, 2023).

Moreover, the response of leaf R_{CO_2} over very wide T ranges (e.g. 10–45°C, Heskell *et al.*, 2016) has also become popular (Fig. S1). In such studies, ln-transformed R_{CO_2} is typically plotted as a function of T and a second-order polynomial model is often (Fig. S1) fitted over the entire T range: $\ln R_{CO_2} = a + bT + cT^2$, where $Q_{10} = e^{10 \times (b - (2 \times cT))}$ with the 'b' coefficient being the slope of ln R_{CO_2} as function of T at 0°C and the 'c' coefficient representing any quadratic nonlinearity in the slope of ln R_{CO_2} with increasing measuring T. We understand the motivation of this approach as it can capture the nonlinearity of a general $Q_{10}(T)$ -relationship (O'Sullivan *et al.*, 2013; Heskell *et al.*, 2016). However, it is a common problem with second-order polynomial fits that the 'b' and 'c' regression coefficients are colinearly dependent, which can lead to incorrect conclusions about 'b' and 'c' (Chatterjee & Greenwood, 1990). Hence, with this analytical approach the estimated values of Q_{10} at low T can be artificially influenced by both: (1) any variability in the 'c' regression coefficient (Fig. 1c) that may arise from both measurement errors and potential systematic biological variation between the type of data included in the overall second-order polynomial fits; and (2) potential underlying physiological, biochemical, and physical mechanisms of Q_{10} of leaf R_{CO_2} that only are relevant at high T (Atkin & Tjoelker, 2003; Kruse *et al.*, 2008). Therefore, the approach of using very wide T ranges (including very high T) can be difficult to apply in attempts to study how underlying physiological, biochemical, and physical mechanisms of Q_{10} of leaf R_{CO_2} may change at different T ranges (Atkin & Tjoelker, 2003; Kruse *et al.*, 2008).

We therefore suggest that leaf Q_{10} of night-time R_{CO_2} is approximated by linear plots of ln R_{CO_2} as a function of T for each individual narrow T range (e.g. max 10°C ranges, Figs 1d, S2–S4). We recommend at least four different Ts for any given T range studied. This is because when we examined examples of the linear plots of ln R_{CO_2} as a function of T that did not exhibit a slope statistically significantly different from zero (Fig. S4), then with only three different Ts for a given T range it is impossible to decide with certainty which of the combinations of T and R_{CO_2} is an outlier due to for example measurement errors. That is why also many of our own estimates of Q_{10} (Fig. S4) had to be omitted (see also Methods S1) in Fig. 2. Preferably, when it is possible for the experimentalist, we recommend the high-resolution measurement approaches of for example O'Sullivan *et al.* (2013) and Heskell *et al.* (2016), which can enable very detailed linear plots of ln R_{CO_2} as a function of T for each individual narrow T range (Fig. 1d).

A general $Q_{10}(T)$ -relationship representing night-time leaf R_{CO_2}

As such, for the general $Q_{10}(T)$ -relationship representing night-time leaf R_{CO_2} we present in Fig. 2, we only use studies where measurements of Q_{10} of night-time leaf R_{CO_2} were conducted at night-time alone, only in response to very short-term temperature manipulations (i.e. instantaneous Q_{10}

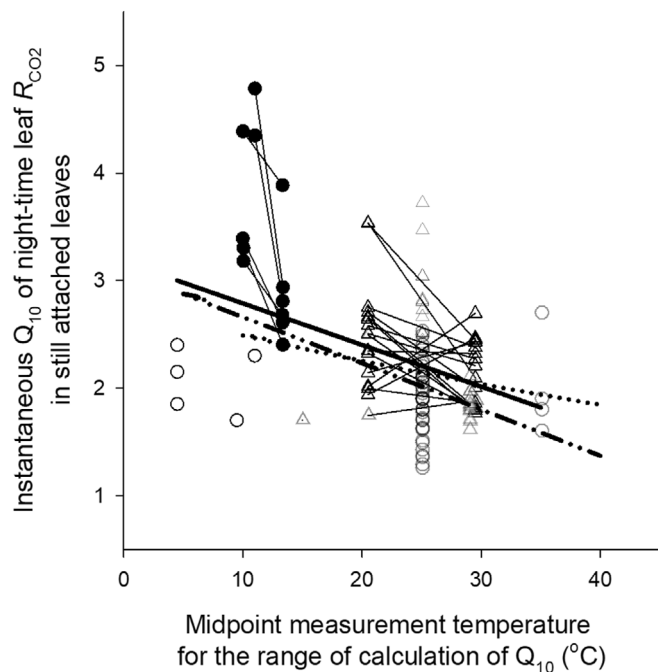


Fig. 2 General $Q_{10}(T)$ -relationship across species for night-time leaf R_{CO_2} . Own field-based data from Denmark are shown as closed circles (only values of Q_{10} included here are from Denmark, as most of our United Kingdom data did not fulfil our own criteria of statistically significantly different slope ($\ln(R_{CO_2})/T$) from zero). Previously published data are shown as open symbols (circles represent field data and triangles represent growth cabinet studies). For details on species and Q_{10} values, see Table S1. For criteria for included data, see Methods S1. Species examined at more than one midpoint temperature are shown with connecting lines. Linear regression $Q_{10} = 3.17 \pm 0.20$ (mean \pm SE, $P < 0.0001$) – 0.04 ± 0.01 (mean \pm SE, $P < 0.0001$) $\times T$, $R^2 = 0.1516$, $n = 127$, 24 species (full thick line). For comparison are shown earlier relationships by Atkin & Tjoelker (2003) without indications of whether Q_{10} was measured at day or at night (dotted-dashed line) and by Heskell *et al.* (2016) with only daytime measurements of Q_{10} (dotted line).

instead of an apparent Q_{10}), and on still attached leaves. This first general $Q_{10}(T)$ -relationship of only night-time leaf R_{CO_2} (Fig. 2) is steeper than previous large-scale studies (Heskell *et al.*, 2016), in which daytime dark-adapted leaf R_{CO_2} was measured instead. Moreover, the values of Q_{10} across species at night-time $T < c.$ 30°C are higher than previously assumed based on measurements without information about the timing of dark-adapted measurements (Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003).

Concluding remarks and perspectives

The data underlying Fig. 2 reconfirm the assumption (Wager, 1941; Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003; Atkin *et al.*, 2005a, b; Heskell *et al.*, 2016) of a general $Q_{10}(T)$ -relationship of night-time leaf R_{CO_2} . However, the data also represent different species for the different T ranges, times of year, latitudes, ages, and environmental conditions. Thus, even though, we have limited the data to Q_{10} of only night-time leaf R_{CO_2} we still do not consider to have a sufficient set of data to comfortably say this is a final general

$Q_{10}(T)$ -relationship of night-time leaf R_{CO_2} , which can be used for studies of the relative control of the different underlying physiological, biochemical, and physical mechanisms of Q_{10} of leaf R_{CO_2} may change at different T ranges (Atkin & Tjoelker, 2003; Kruse *et al.*, 2008). At best, this general $Q_{10}(T)$ -relationship of night-time leaf R_{CO_2} (Fig. 2) may be used as very crude proxy for modelling of leaf R_{CO_2} across different species, T ranges, times of year, latitudes, different ages, and environmental conditions in the absence of an own $Q_{10}(T)$ -relationship of night-time leaf R_{CO_2} .

To further our understanding of the potential shift in relative control by underlying physiological, biochemical, and physical mechanisms of Q_{10} of night-time leaf R_{CO_2} (Atkin & Tjoelker, 2003; Kruse *et al.*, 2008) more data representing different species, the different T ranges, different times of year, different latitudes, different ages, and different environmental conditions is needed and when collecting such data, it is necessary to be very mindful of the timing of measurements, measurement approach, and analytical approach as discussed in earlier sections. Furthermore, we encourage limiting future studies to only include T ranges relevant (Kruse *et al.*, 2008) for night-time.

Mechanistic studies at different T ranges are traditionally studied in plants by measuring respiratory O_2 uptake (cf. Atkin & Tjoelker, 2003). However, potential mechanisms underlying the Q_{10} of the rate of leaf respiratory mitochondrial ATP production (i.e. O_2 uptake, R_{O_2}) cannot be directly translated to that of R_{CO_2} . This is because leaf respiratory CO_2 efflux and O_2 uptake are not tightly coupled (Kruse *et al.*, 2008; Bruhn *et al.*, 2024) as the respiratory quotient (ratio of CO_2 efflux to O_2 uptake) is varying on a diel scale, even at a constant T (Bruhn *et al.*, 2024). Indeed, the Q_{10} of leaf R_{CO_2} differs from that of leaf R_{O_2} (Tcherkez *et al.*, 2003; Kruse *et al.*, 2008). Therefore, we encourage more mechanistic work performed with leaf R_{CO_2} and this will require some careful ingenuity to replicate some of the hitherto insights from R_{O_2} (Atkin & Tjoelker, 2003).

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Competing interests

None declared.

Author contributions

DB conceptualised the idea, conducted the analyses, and wrote the manuscript. AG and PP conducted the field measurements in the UK and DK, respectively. PP did the statistical tests underlying Figs S2 and S3. DB, AG, PP and LM all edited the manuscript and devised the experimental design.

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Data availability

Data are available in figure texts to Figs S2–S4, Table S1 and Notes S1–S2.

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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 Timing of different trends within publications on temperature sensitivity of leaf R_{CO_2} from 1992 to 2023.

Fig. S2 Early vs late – Q₁₀.

Fig. S3 Cooling vs heating – Q₁₀.

Fig. S4 Measurement temperature effect on Q₁₀.

Methods S1 Supporting methods.

Table S1 Data underlying Fig. 2.

Table S2 Night-time ambient temperatures during measurements in Denmark.

Notes S1 References underlying Fig. S1.

Notes S2 References underlying Methods S1 & Fig. 2 (Table S1).

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