

Assessing the relevant time frame for temperature acclimation of leaf dark respiration: A test with 10 boreal and temperate species

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Abstract

Plants often adjust their leaf mitochondrial (“dark”) respiration (R_d) measured at a standardized temperature such as 20°C (R_{20}) downward after experiencing warmer temperatures and upward after experiencing cooler temperatures. These responses may help leaves maintain advantageous photosynthetic capacity and/or be a response to recent photosynthate accumulation, and can occur within days after a change in thermal regime. It is not clear, however, how the sensitivity and magnitude of this response change over time, or which time period prior to a given measurement best predicts R_{20} . Nor is it known whether nighttime, daytime, or 24-hour temperatures should be most influential. To address these issues, we used data from 1620 R_d temperature response curves of 10 temperate and boreal tree species in a long-term field experiment in Minnesota, USA to assess how the observed nearly complete acclimation of R_{20} was related to past temperatures during periods of differing lengths. We hypothesized that R_{20} would be best related to prior midday temperatures associated with both photosynthetic biochemistry and peak carbon uptake rates that drive carbohydrate accumulation. Inconsistent with this hypothesis, prior night temperatures were the best predictors of R_{20} for all species. We had also hypothesized that recent (prior 3–10 days) temperatures should best predict R_{20} because they likely have stronger residual impacts on leaf-level physiology than periods extending further back in time, whereas a prior 1- to 2-day period might be a span shorter than one to which photosynthetic capacity and R_d adjust. There was little to no support for this idea, as for angiosperms, long time windows (prior 30–60 nights) were the best predictors, while for gymnosperms both near-term (prior 3–8 nights for pines, prior 10–14 nights for spruce/fir) and longer-term periods (prior 45 nights) were the best predictors. The importance of nighttime temperatures, the relatively long “time-averaging” that best explained acclimation, and dual peaks of temporal acclimation responsiveness in some species were all results that were unanticipated.

KEYWORDS

acclimation, B4WarmED, boreal, carbon cycle, night temperature, respiration (R_{20}), temperate

1 | INTRODUCTION

Leaf dark respiration (R_d) is enzyme-catalyzed and therefore temperature-dependent. On instantaneous to short-term time scales (minutes to hours), R_d increases near-exponentially with temperature (Heskel et al., 2016; Tjoelker et al., 2001) and is regulated in part by the temperature dependence of reaction rates of multiple enzymes involved in cytosolic and mitochondrial respiratory pathways (Atkin et al., 2005). Land plant R_d is a major component of the carbon cycle, releasing ca. 30 Pg C year⁻¹ to the atmosphere, far more than from all sources of anthropogenic CO₂ emissions (Heskel et al., 2016; Huntingford et al., 2017; Tjoelker et al., 2001). Because of the temperature sensitivity of R_d , it has been proposed that global warming will increase the magnitude of this respiration and accelerate climate change (Cox et al., 2000; Huntingford et al., 2013).

However, leaves often acclimate over longer time periods (days, weeks, and months), that is, adjust the elevation of their entire temperature response curve or their R_d at a standardized measurement temperature, $R_{d, \text{standard}}$ (which we will use as a proxy for the entire temperature response curve in this paper) to a lower rate after experiencing warmer temperatures and to a higher rate after experiencing cooler temperatures (Atkin et al., 2015; Reich et al., 2016; Slot & Kitajima, 2015; Togashi et al., 2018; Vanderwel et al., 2015). Such acclimation can dampen the magnitude of the positive feedback from rising temperatures (Huntingford et al., 2017; Reich et al., 2016; Smith et al., 2016, 2019; Wythers et al., 2013). Important knowledge gaps remain including ignorance about how R_d acclimation (i.e., $R_{d, \text{standard}}$) relates to temperatures experienced across different time frames and durations. This matters to how acclimation is accounted for in models, because how quickly plants acclimate R to temperature change can have large impacts on both the amount of seasonal variability of realized R_d and the total annual cumulative respiratory flux (Atkin et al., 2000). Nonetheless, because of the observed linkages between $R_{d, \text{standard}}$ and prior temperatures on a week to 10-day period, several modeling studies have used the prior 10-day period for expressing or simulating acclimation (Atkin et al., 2008; Lombardozzi et al., 2015; Smith & Dukes, 2013), despite weak evidence in favor of such a choice over any different time window. Remedying this will require evaluating the time period that is most strongly related to R_d temperature acclimation. Addressing that issue is the focus of our paper.

There is both theoretical and empirical evidence suggesting that leaf respiration is closely coupled with photosynthetic activity, although it could also be related to growth and/or other controls of carbohydrate accumulation. First, acclimation of R_d acts to optimize and maintain photosynthetic capacity in the face of temperature variability (Noguchi & Yoshida, 2008; O'Leary et al., 2019; Reich et al., 1998; Smith & Dukes, 2017; Wang et al., 2020). R_d supports metabolic processes of photosynthesis such as protein turnover, phloem loading, the maintenance of ion gradients between cellular compartments, and the turnover of phospholipid membranes

(Atkin et al., 2005; Wang et al., 2020). As Rubisco represents a large fraction of total leaf protein, R_d is expected to scale with maximum carboxylation capacity (V_{cmax}) or with proxies such as leaf nitrogen content or concentration, as well as with sugars, relevant to both substrate availability and ATP demand (Reich et al., 1998; Scafaro et al., 2017; Tjoelker et al., 2008; Wang et al., 2020). Given that the rate of photosynthesis is temperature-dependent, V_{cmax} (assessed at a standardized temperature) may have a general tendency to adjust to average daytime conditions so that the electron transport- and Rubisco-limited photosynthetic rates are co-limiting (Maire et al., 2012; Wang et al., 2020); further R_d acclimation may help maintain stable and optimal photosynthetic capacity (Wang et al., 2020) and a more stable realized R_d : GPP ratio than would occur otherwise (Drake et al., 2016). Second, some studies (Hartley et al., 2006; Werten & Teskey, 2008; Whitehead et al., 2004) but not others (e.g., Drake et al., 2016) found leaf respiration rates to be well correlated with the rate of photosynthesis on the preceding day, presumably via a substrate effect on respiratory metabolism (Tjoelker et al., 2008; Werten & Teskey, 2008).

Individual respiratory processes have different dynamics in terms of temporal changes in response to temperature variation (Armstrong et al., 2008), suggesting that expectation of a single, simple linkage between acclimation and prior temperature windows might be unfounded. However, when leaves are exposed to marked temperature variability under controlled conditions, R_d can acclimate in as little as 1–3 days (Atkin et al., 2000; Bolstad et al., 2003) and there is evidence of acclimation in as little as a week under strongly changing field conditions (Lee et al., 2005). This suggests the potential for rapid acclimation. Moreover, rapid acclimation of R_d may reflect relatively short to intermediate scale variation in other aspects of leaf morphology and chemistry such as leaf mass per area (LMA), nitrogen concentration (%N), and non-structural carbohydrate contents (Gorsuch et al., 2010; Lee et al., 2005; O'Leary et al., 2017; Tjoelker et al., 2008; Will, 2000). As a result of such observations, acclimation is often quantified using a short time window (2–10 days) of averaged prior temperature (Atkin, Edwards, et al., 2000; Lee et al., 2005; Ow et al., 2010; Reich et al., 2016; Tjoelker et al., 2008). However, which specific prior time period it is best related to—and whether it is day or night temperature that matters—is relatively little explored (Searle et al., 2011).

In this paper, we use a large data set of 10 tree species grown under field conditions (Reich et al., 2016) to explore which time period (day or night) and for what duration seems most relevant to observed R_d temperature acclimation. There was strong evidence of Type II acclimation (a downward shift of the intercept with no change in the slope of the log₁₀ relationship of R_d to temperature) in all species and no evidence of Type I acclimation in any species (Reich et al., 2016; Wei et al., 2017). In other prior work from this same study, the focal species showed homeostasis of photosynthetic capacity measured at a standardized temperature (e.g., $V_{\text{cmax-25}^\circ\text{C}}$) across both experimental and seasonal temperature variation (Reich et al., 2018; Stefanski et al., 2020). If, as

hypothesized from research with other species, R_{20} acclimates to temperature as part of a process that optimizes photosynthesis and does so in a fashion that maintains a relatively stable ratio (on weekly or longer, not daily, time scales) of photosynthetic capacity to realized R_d (Drake et al., 2016; Wang et al., 2020), then R_{20} would acclimate to temperature variation to compensate for the enzymatic temperature sensitivity of R_d , in terms of realized R_d rates and R_d :A ratios.

Among many unanswered questions, herein we focus on two involving the timing and conditions that serve as cues for acclimating R_d , drive the metabolic processes involved in acclimation, or both. We ask what prior time period best predicts variation in R_{20} and what aspect of diurnal temperature variation (daytime, nighttime) plays the largest role? To assess this, we regressed R_{20} against prior time windows of different length for mean nighttime, daytime (total), daytime peak photosynthetic, and 24-hour average temperatures. Although correlation does not suggest causation, it seems logical to interpret the highest correlation and greatest sensitivity (of R_{20} to a given temperature for a given time window) as indicative of likely importance relative to the R_{20} acclimation process (as done previously by Searle et al., 2011). To our knowledge, little other empirical work has been done to address these questions; a similar but perhaps not as extreme a lack of empirical data exists apropos to the appropriate time scale for temperature acclimation of photosynthesis (Dietze, 2014).

We hypothesized (H1) that recently (prior 3–10 days) experienced temperatures should best predict R_{20} because they are more likely to have residual impact on leaf-level physiology than periods that extend further back in time and also should be more useful predictors of near future temperature as well. We expected the immediate 1–2 days prior to not be as good a predictor of R_{20} because it might represent a period shorter than one to which photosynthetic capacity or R_d adjusts (Atkin et al., 2008; Campbell et al., 2007; Dietze, 2014), in part because processes and properties thought to influence R_d (e.g., non-structural carbohydrates, LMA, N), likely take longer than that to adjust. We also predicted (H2) that daytime temperatures, and especially midday temperatures during periods of higher irradiance and thus higher photosynthesis (e.g., 09:00–15:00 h solar time) will better predict R_{20} than either night or 24-hour average temperatures, based on the premise that R_d acclimation is associated with photosynthetic biochemistry (Wang et al., 2020), which itself should be adjusting more to daytime than nighttime temperature.

To assess our hypotheses, we used data from 1620 R_d temperature-response curves made for 10 tree species grown under field conditions. The measurements were made in the context of a long-term warming experiment, and prior papers examined the acclimation of respiration to both experimentally manipulated temperatures and seasonal variation in temperature (Reich et al., 2016; Wei et al., 2017). In all species, strong Type II acclimation was observed, with similar results seen in different seasons and years. Moreover, acclimation responses to experimentally manipulated temperatures and seasonal variation in

temperature were similar. However, neither of those papers examined the time periods (day vs. night, duration of influential time windows) most relevant to acclimation in general, which is the focus of this current paper.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was done using the B4WarmED experiment (Reich et al., 2016) implemented at both the Cloquet Forestry Center (CFC) at Cloquet, MN, USA (46°31' N, 92°30' W) and at the Hubachek Wilderness Research Center (HWRC) near Ely, MN, USA (47°55' N, 92°30' W). Mean annual precipitation and temperature (1973–2008) were 783 mm and 4.8°C at CFC and 726 mm and 2.6°C at the nearest weather stations to HWRC, respectively. The weather and climate data used in this paper, however, were acquired from continuous monitoring at each of the 48 plots used in this study (Rich et al., 2015). The experiments at both sites were conducted on coarse-textured upland soils in mixed *Populus tremuloides*–*Betula papyrifera*–*Abies balsamea* stands (with stand ages of 40–60 years) in both understory (5–10% full light) and recently cleared (40–60% full light) conditions. Respiration measurements were made for ~1500 individuals of 10 common temperate-boreal tree species planted within the B4WarmED experiment as seedlings in 2008.

2.2 | Experimental design

The details of experimental design are described by Reich et al., (2015, 2016) and Rich et al., (2015). The experiment had a 2 site × 2 habitat × 3 warming treatment factorial design with six replicates, for a total of 72 circular plots 3 m in diameter. The treatments included three levels of simultaneous plant and soil warming; ambient temperatures and both +1.7°C and +3.4°C above ambient day and night temperatures throughout the entire growing season. All treatments included soil heating cables (un electrified cables in the ambient plots). The heating treatment was implemented during the 2009–2013 growing seasons with a synchronized above- and belowground open-air system (i.e., without chambers) via feedback controls that acted concurrently and independently at the plot scale to maintain a fixed temperature differential from ambient conditions. Seedlings of 10 tree species were planted in each plot into the existing ground vegetation of herbs and shrubs in 2008. The seedlings were obtained from the Minnesota Department of Natural Resources (Reich et al., 2015; Rich et al., 2015). For this study, we used all 48 plots in the ambient and +3.4°C above ambient treatments. Warming treatments were near target temperature elevations in all years (Reich et al., 2015, 2016; Rich et al., 2015). Warming treatments increased vapor pressure deficits in the air within the canopy to the extent expected in a system with similar total water content (Reich et al.,

2018) and higher temperatures also caused decreased soil water content due to higher evapotranspiration driven by those higher vapor pressure deficits (Reich et al., 2018; Rich et al., 2015).

2.3 | Measurement of leaf respiration temperature response curves

Temperature response curves ($n = 1620$) of leaf respiration were measured on detached foliage sampled from June to September each year and across the years 2009–2013 (Reich et al., 2016). Fully expanded, healthy current-year leaves were collected each morning and were immediately inserted into floral water pik tubes to keep them hydrated throughout the day. The leaves were then transported to a nearby laboratory and transferred to a darkened growth chamber that was able to maintain a broad range of temperatures. Temperature response curves were measured from 12 to 37°C at increments of 5°C by adjusting the air temperatures of the growth chamber. Measurements were made for all 10 species sampled from ambient and warmed plots at both sites and in both canopy conditions. Respiration temperature response curves were developed based on measurements at 12, 17, 22, 27, 32, and 37°C. Given greater logistical challenges in measuring respiration of conifer needles than of angiosperm broad leaves, work with the former species was done at a lower level of frequency.

The dark respiration rate was measured using an infrared gas analyzer (Li-6400 portable photosynthesis system; Li-Cor, Lincoln, NE, USA) with a standard 2 × 3 cm leaf chamber, operated in an open configuration with a flow rate of 300–500 $\mu\text{mol s}^{-1}$ and a CO_2 concentration of 400 $\mu\text{mol mol}^{-1}$. The leaf chamber was placed inside the growth chamber, and the leaf temperature in the cuvette was set to correspond to the temperature in the growth chamber. The leaf was allowed to stabilize at the new temperature for a minimum of 10 min before the dark respiration was measured, and the leaf was then clamped in the leaf chamber for the measurement. Three measurements were logged at 15 second intervals after the readings had stabilized and were averaged for each temperature. Humidity within the leaf chamber was controlled to the best of our ability; to keep relative humidity between 35% and 70%, and to avoid condensation. We routed incoming air through desiccant at low temperatures to keep relative humidity lower, and allowed additional humidified incoming air into the chamber at higher temperatures when humidity levels were lower. The measurements were completed within 3–4 h. Dark respiration rates of detached leaves are relatively stable under these conditions for several hours or longer (Slot et al., 2014; Tjoelker et al., 2008).

2.4 | Data analyses

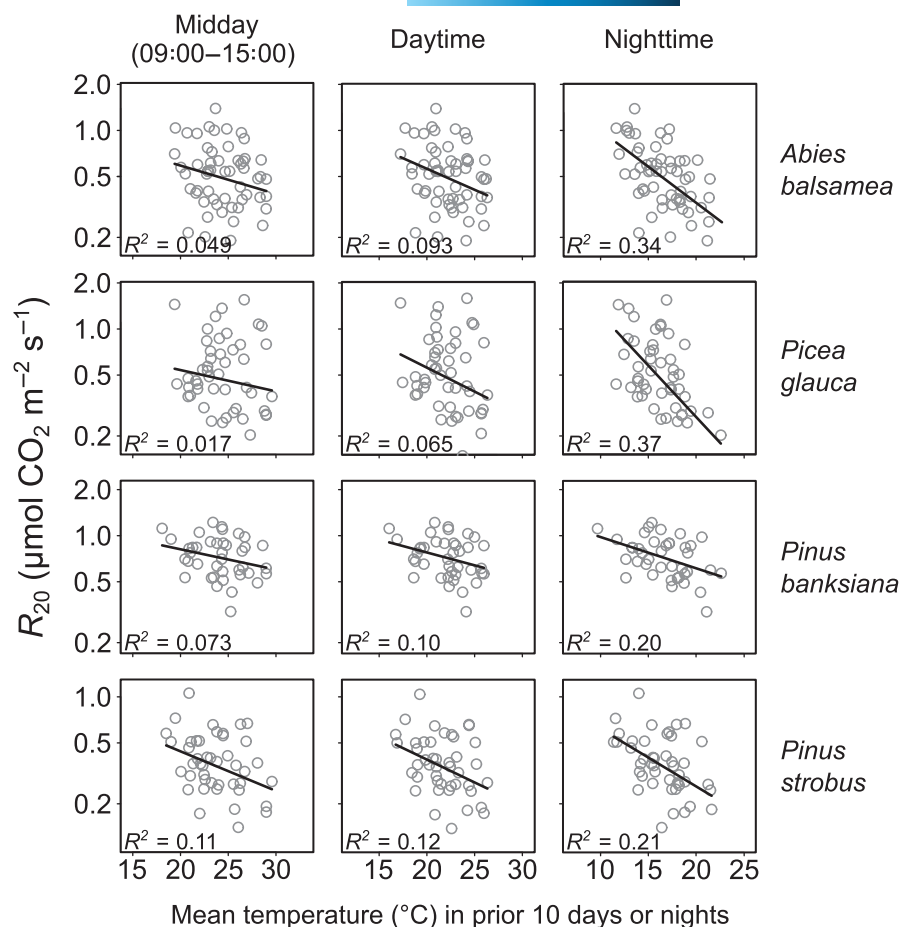
Comparisons among different models showed that fixed Q_{10} and Arrhenius models provided the most reasonable statistical approach, and nearly identical fits, for our short-term respiration–temperature

response curves (mean R^2 for all 1620 temperature response curves = 0.93 for both models; Reich et al., 2016). We therefore report the respiration rate at a standard measurement temperature of 20°C (R_{20}) calculated from the fixed Q_{10} temperature response equation for every leaf. R_{20} values were $\log_{10}$ -transformed to fit assumptions of a normal distribution of residuals and to linearize the large majority of bivariate fits with prior temperatures, simplifying the forms of, and the comparisons among, assessed relationships. We examined the relationship, by species, between $\log_{10} R_{20}$ (R_{20} hereafter) and various metrics of mean temperature prior to the time of measurement. These metrics included prior daytime, midday (09:00–15:00 h), nighttime, and 24-hour values, averaged (across all mean 30 min temperature averages) for the prior 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 15, 20, 25, 30, 45, 60, and 90 days (or nights). Daytime was defined as anytime the sun elevation was >0 degrees (i.e., above the horizon). Although not all relationships were best described by linear fits, most were, so for comparative purposes we used linear fits for all. As the relationships were generally unaffected by site, habitat, or temperature treatment (Reich et al., 2016; Wei et al., 2017), we report data by species pooling data across these other sources of variation. We also tested both whether models with multiple prior time windows improved predictions of R_{20} and whether other environmental conditions (vapor pressure deficit or Dra soil water content) influenced the response of R_{20} to prior temperatures. Finally, as the relationship of R_{20} to previously experienced temperatures of differing time windows was similar for plants in ambient and warmed treatments (Reich et al., 2016), we lump warming treatments together in the current paper; note however that the plants in the different warming treatments experienced different prior temperatures, even when sampled on the same day. All data analyses used JMP PRO 15.1.0 (SAS Institute, Cary, USA).

3 | RESULTS

Substantial and consistent respiratory acclimation to temperature occurred, as noted by lower R_{20} when prior time periods were warm than when they were cool (Figures 1–5). Across all species and time windows (i.e., numbers of prior days or nights), R_{20} was better related to prior nighttime temperatures than to prior daytime or 24-hour average temperatures (Table 1, Figures 1–3), other than in a few instances. The differences in explanatory power were more pronounced for longer time windows of 10 or more days or nights (Figure 3), for which nighttime temperatures explained between ~20–25% of R_{20} variance but daytime and midday temperatures explained only 6–10% or 3–5%, respectively, of variation in R_{20} . These differences in the strength of the relationship of R_{20} to prior nighttime versus daytime temperatures occurred despite strong correlations ($R > 0.8$) between nighttime and daytime temperatures for all prior time-window lengths. Relationships of R_{20} to minimum and maximum daily temperatures were similar or slightly poorer than relations to mean night and day temperatures, respectively (data not shown), at all time windows.

FIGURE 1 Relationship between the respiration rate at a measurement temperature of 20°C (R_{20}) and three measures of prior 10 day or night temperatures for four gymnosperm tree species. All the panels maintain the same proportion for both axes (respiration and temperature), making the slopes directly comparable. Vertical axes are in logarithmic scale



Relationships of R_{20} to prior midday or daytime temperatures had only a weak temporal pattern (Figure 3). On average across the 10 species, the correlation with prior night temperatures (T_{night}) grew stronger as longer prior periods were considered (Figure 3), with $R^2 = 0.11$ for $T_{2 \text{ nights}}$, $R^2 = 0.19$ for $T_{10 \text{ nights}}$, and $R^2 = 0.24$ for $T_{30 \text{ nights}}$. Responses to the 24-hour temperature time windows were intermediate between those for day temperature alone or night temperatures alone.

Individual species, and species groups, also differed substantially in how both the fit and slope of the relationship of R_{20} to T_{night} varied depending on the length of prior period considered (Figures 4–6, Table 1). All four conifers showed two peaks for the relationship, one peak at a short time window of either ≈ 3 –8 or ≈ 10 –14 nights, followed by a weaker relationship to T_{night} of prior 15–20 nights, and another stronger peak at 30–45 nights (Figure 6). In both *A. balsamea* and *P. glauca*, R_{20} remained strongly correlated ($R^2 > 0.30$) out to a 90-night T_{night} window, whereas for the two pines, the signal degraded moving from 45- to 90-night windows. The species also differed in the time windows that showed the strongest $R_{20} - T_{\text{night}}$ relationships; 3–8 nights for *P. strobus*, 5 or 45 nights for *P. banksiana*, ≈ 10 or 25–60 for *P. glauca*, and 30–60 nights for *A. balsamea*.

The six deciduous angiosperms did not show any pronounced bimodality of the R_{20} to T_{night} relationship across prior time windows. They all showed increases in R^2 and steeper (more negative)

slopes as the time window was extended to at least 30 nights, but diverged in their patterns over longer time-window lengths (Figure 6). *A. rubrum*, *Q. macrocarpa*, and *B. papyrifera* had their strongest relationship of R_{20} to T_{night} for a 30-night window, with poorer fits using longer windows. In contrast, *A. saccharum*, *P. tremuloides*, and *Q. rubra* retained strong correlations of R_{20} to prior average mean T_{night} as far as 90 nights prior to R_d measurement. In the deciduous species, for most measured leaves a 75- or 90-day or night period prior to the measurement date included some time period prior to leaf formation, perhaps contributing to weaker relations of acclimation to the longest prior time periods.

We also were interested in whether more complex models with multiple time windows or with additional variables such as VPD or VWC better explained R_{20} acclimation. For most of the ten species, the best R_{20} to T_{night} models with two or more terms (with each term, a temperature of a window of different length) were notably better than those using a single time window, based on variance explained and BIC (Table 2). For the four coniferous species, the proportion explained increased substantially (by between 25% and 40% additional total variance explained); for the angiosperms, the more complex models offered negligible to modest improvements. This is consistent with patterns shown in Figure 6; not surprisingly given multiple peaks, for the conifers information for multiple time frames of markedly different lengths helped improved predictions of acclimation of R_{20} .

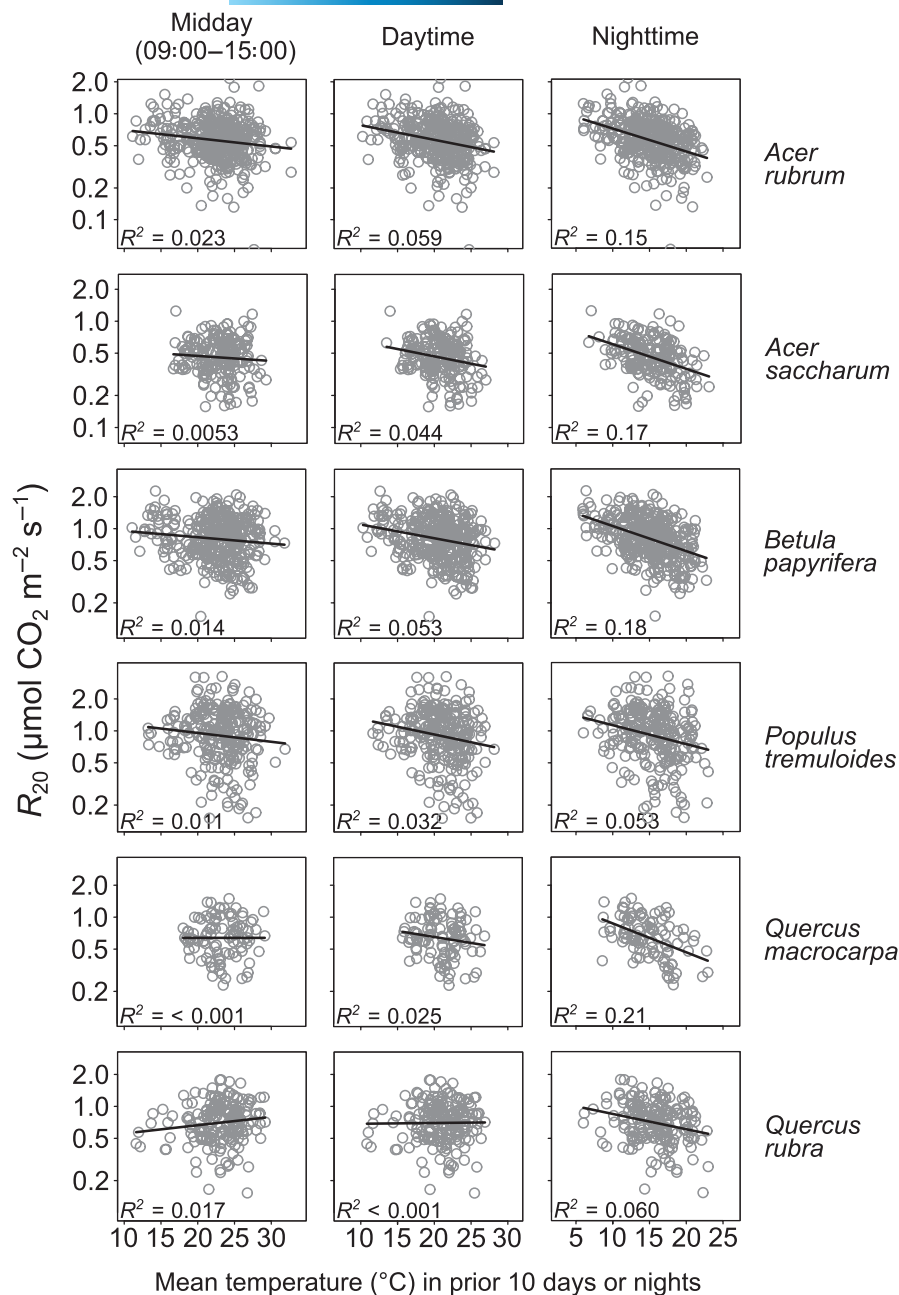


FIGURE 2 Relationship between the respiration rate at a measurement temperature of 20°C (R_{20}) and three measures of prior 10 day or night temperatures for six angiosperm tree species. All panels maintain the same proportion for both axes (respiration and temperature), making the slopes directly comparable. Vertical axes are in logarithmic scale

We also examined whether prior VPD or VWC influenced respiratory acclimation, although modest to strong positive correlations of temperature and VPD (for day, night, or 24-hour periods) and negative correlations of both with VWC complicate efforts to disentangle their possible impacts on R_{20} acclimation. First, using data for all species pooled, we chose four prior time windows (prior 1, 8, 15, and 30 days or nights) that reflect much of the variation assessed in the study and tested all models that included T_{night} , T_{day} , VPD (mean 24-hour), and VWC (mean 24-hour). There were 16 terms in total and we evaluated all models with 1–4 terms per model. The best model by AIC and BIC criteria included $T_{30 \text{ nights}}$, $T_{30 \text{ days}}$, $\text{VWC}_{8 \text{ days}}$, and $\text{VPD}_{30 \text{ days}}$ (all < 0.001); with R_{20} decreasing with increasing $T_{30 \text{ nights}}$ or $\text{VPD}_{30 \text{ days}}$ but increasing with increasing $T_{30 \text{ days}}$ and $\text{VWC}_{8 \text{ days}}$ (Table S1). Of the total variance explained, $T_{30 \text{ nights}}$ explained 65%, $T_{30 \text{ days}}$ 23%, $\text{VPD}_{30 \text{ days}}$ 9%, and $\text{VWC}_{8 \text{ days}}$ 3%. Second for each

species individually we also examined models that included four terms, $T_{30 \text{ nights}}$, $T_{30 \text{ days}}$, $\text{VWC}_{30 \text{ days}}$, and $\text{VPD}_{30 \text{ days}}$. For the 10 species, the average variance in R_{20} explained was 40%. In all species, R_{20} decreased with $T_{30 \text{ nights}}$ ($p < .05$), and in all but one case $T_{30 \text{ nights}}$ explained more of the variation than any other term ($T_{30 \text{ nights}}$ accounted for between 30 and 70% of the explained variance among the 10 species; Table S2). $T_{30 \text{ days}}$ was positively related to R_{20} in 9 of 10 species ($p < .05$; see Discussion for possible explanations for this shift compared to its bivariate relationship with R_{20}) and explained one-fifth to three-fifths as much of the variance as $T_{30 \text{ nights}}$. In 5 of 10 species $\text{VPD}_{30 \text{ days}}$ was negatively related ($p < .05$) to R_{20} and in those five cases accounted on average for about one-fifth of the explained variance. In one species, $\text{VWC}_{30 \text{ days}}$ was positively related ($p = .057$) with R_{20} , and in that case accounted for about one-sixth of explained variance. Both the combined pooled model and

individual species models indicate that night temperature was the dominant driver of R_{20} acclimation, but that other aspects of the environment also matter. Additionally, models including night and day

temperatures, VWC, and VPD at time windows other than 30 days (e.g., 5, 10, or 20) were similar to the 30-day model in terms of rank order of important drivers and their direction.

Although the R_{20} to T_{night} relationship for a single prior night was weak on average (mean $R^2 = 0.08$ across species) and much weaker than for longer time windows in all species, it was statistically significant for 9 of the 10 species. This could indicate that a single night's thermal conditions influence respiratory acclimation; alternately, those significant relationships might have occurred because the single prior night temperature substantially co-varied with temperatures over longer time periods that might be more influential on the R_{20} to T_{night} relationship. For example, $T_{1 \text{ night}}$ shares at least 50% information ($R > 0.71$) with prior temperature as long as five nights ($T_{5 \text{ nights}}$) and 40% information with $T_{10 \text{ nights}}$.

The observed relationships of R_{20} to T_{night} demonstrate marked acclimation (Figures 1–5). To characterize the extent of acclimation, we quantified the percent acclimation, that is, the percent reduction in rise of realized R per $^{\circ}\text{C}$ increase in temperature below that which would have occurred given measured Q_{10} , if no acclimation had happened (cf. Reich et al., 2016). For example, if for a 10°C temperature rise, realized R increases by 25% rather than the 100% a Q_{10} of 2 would yield without acclimation, percent acclimation would be 75%; 100% acclimation corresponds to complete homeostasis. On average across the 10 species, the mean and median percent acclimation

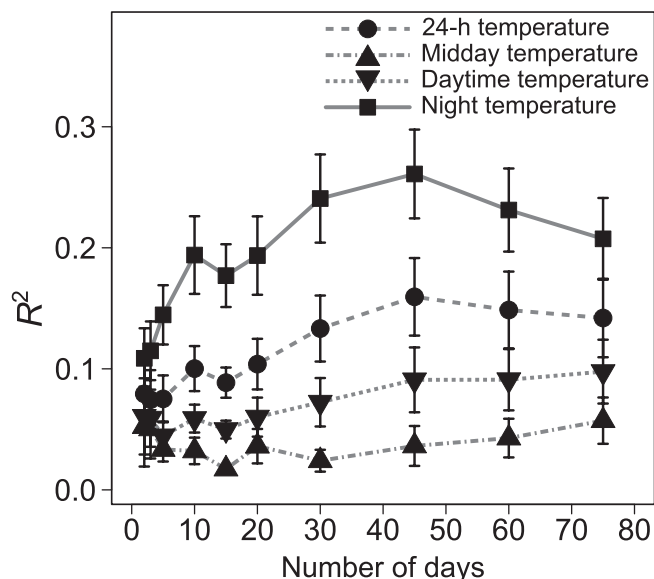


FIGURE 3 Mean R^2 ($\pm$ SE) among all 10 species of the relationship of $\log_{10} R_{20}$ vs. different measures of prior temperature for different time windows (numbers of prior days or nights)

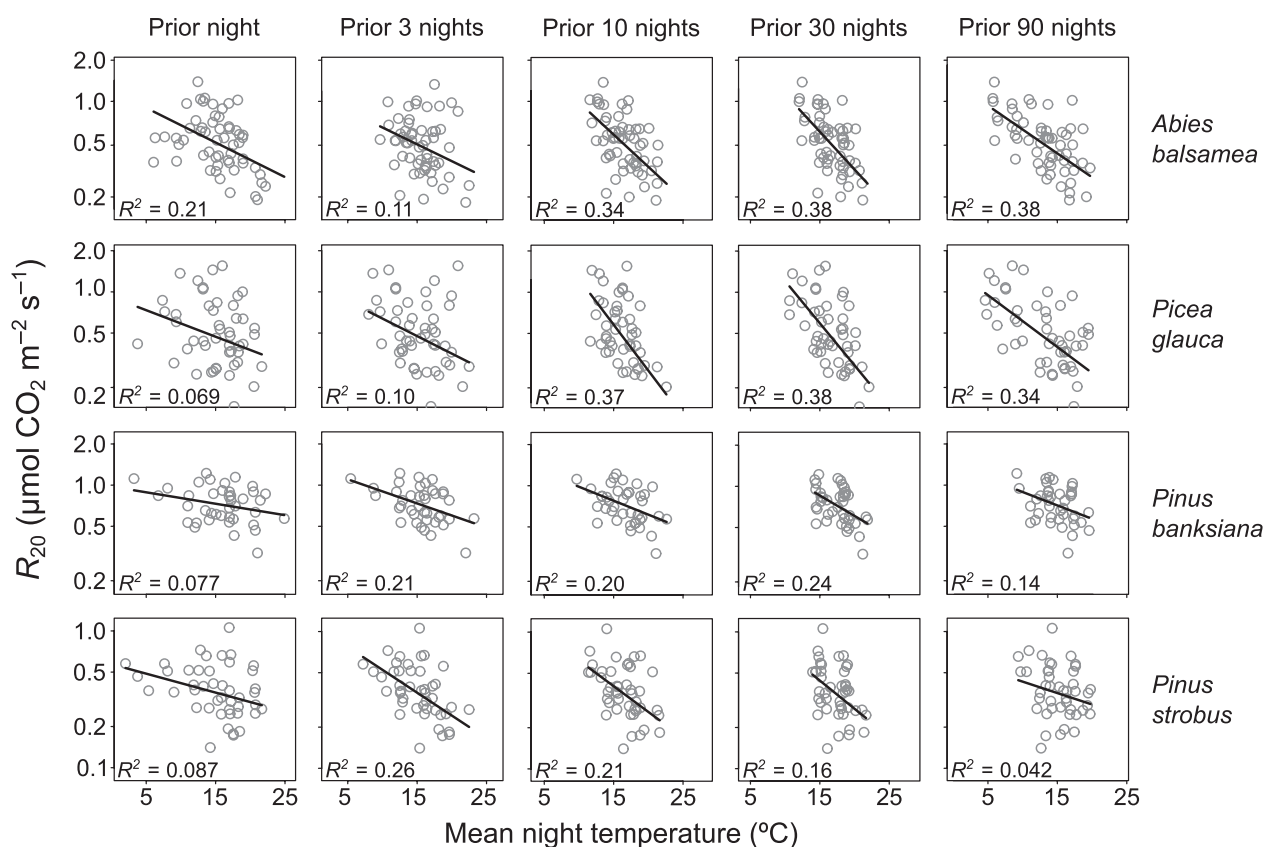


FIGURE 4 Relationship of R_{20} vs. prior night temperature for different time windows (numbers of prior nights) for four coniferous species. All panels maintain the same proportion for both axes (respiration and temperature), making the slopes directly comparable. Vertical axes are in logarithmic scale

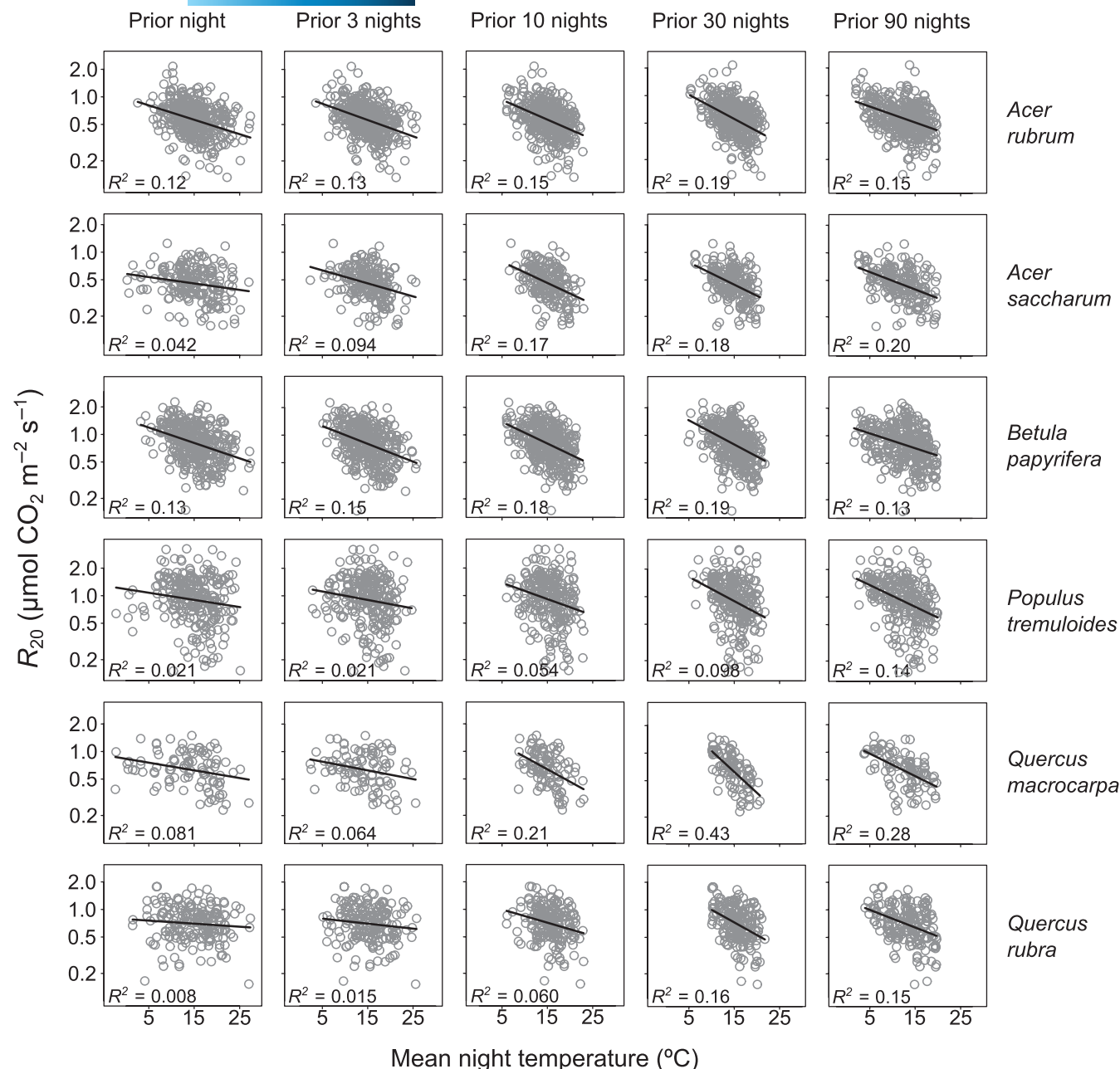


FIGURE 5 Relationship of R_{20} vs. prior night temperature for different time windows (numbers of prior nights) for six angiosperm species. All panels maintain the same proportion for both axes (respiration and temperature), making the slopes directly comparable. Vertical axes are in logarithmic scale

ranged from 69% and 68%, respectively, in relation to prior three nights temperature, increasing with the time-window length to 117% and 104% in relation to the previous 45 nights. Near homeostasis in relation to prior night temperatures is indicated in relation to prior time windows ranging from 10 to 45 nights.

4 | DISCUSSION

Respiration is a key component of the carbon cycle and therefore its accurate representation in models is critical to evaluating the impacts of global change. Our results help address knowledge gaps regarding

both the period during the 24-hour diel cycle and the length of the prior time window that together most strongly correlate with acclimation. We thought that some prior time period of roughly 3–10 days might best cue respiratory acclimation, being both long enough in duration to enable physiological processes to adjust and by being time-averaged, perhaps a more reliable cue for weather the week or two to come than a single or pair of days or nights. Additionally, given strong evidence for mechanistic and statistical links between R_{standard} and photosynthetic capacity (Noguchi & Yoshida, 2008; Togashi et al., 2018; Wang et al., 2020), we expected R_d acclimation to relate the best to either daytime temperature or 24-hour temperature. In contrast, we hypothesized that 1–2 days might be too short

TABLE 1 Correlation coefficient (R^2) of the relationship between $\log_{10} R_{20}$ and prior temperature, with temperature defined by different times of day and windows of duration. These time windows were selected to cover most of the range examined in this study. Midday = 09:00–15:00 h, day is all daylight hours, night is all nighttime hours, 24 h = mean for all 24 hours. N = number of leaves measured

Species	Time of day	N	Number of prior nights or days				
			3	10	20	30	45
<i>Abies balsamea</i>	Midday	57	0.236	0.049	0.083	0.043	0.111
<i>Abies balsamea</i>	Day	57	0.23	0.093	0.14	0.126	0.206
<i>Abies balsamea</i>	Night	57	0.111	0.34	0.344	0.384	0.414
<i>Abies balsamea</i>	24 h	57	0.173	0.162	0.208	0.224	0.298
<i>Acer rubrum</i>	Midday	364	0.017	0.023	0.017	0.024	0.022
<i>Acer rubrum</i>	Day	364	0.044	0.059	0.072	0.074	0.075
<i>Acer rubrum</i>	Night	364	0.128	0.15	0.168	0.187	0.181
<i>Acer rubrum</i>	24 h	364	0.074	0.086	0.104	0.118	0.121
<i>Acer saccharum</i>	Midday	188	0.002	0.005	0.002	0.003	0.001
<i>Acer saccharum</i>	Day	188	0.017	0.044	0.043	0.041	0.054
<i>Acer saccharum</i>	Night	188	0.094	0.166	0.156	0.179	0.206
<i>Acer saccharum</i>	24 h	188	0.034	0.076	0.077	0.087	0.11
<i>Betula papyrifera</i>	Midday	350	0.004	0.014	0.004	0.002	0
<i>Betula papyrifera</i>	Day	350	0.028	0.053	0.039	0.039	0.034
<i>Betula papyrifera</i>	Night	350	0.148	0.183	0.181	0.193	0.186
<i>Betula papyrifera</i>	24 h	350	0.068	0.095	0.084	0.091	0.088
<i>Picea glauca</i>	Midday	50	0.007	0.017	0.007	0.062	0.141
<i>Picea glauca</i>	Day	50	0	0.065	0.059	0.15	0.236
<i>Picea glauca</i>	Night	50	0.1	0.367	0.267	0.381	0.404
<i>Picea glauca</i>	24 h	50	0.019	0.143	0.129	0.245	0.316
<i>Pinus banksiana</i>	Midday	40	0.067	0.073	0.067	0	0
<i>Pinus banksiana</i>	Day	40	0.102	0.101	0.021	0.013	0.026
<i>Pinus banksiana</i>	Night	40	0.209	0.195	0.146	0.238	0.293
<i>Pinus banksiana</i>	24 h	40	0.157	0.153	0.073	0.096	0.131
<i>Pinus strobus</i>	Midday	45	0.131	0.109	0.131	0.005	0.002
<i>Pinus strobus</i>	Day	45	0.136	0.117	0.008	0	0.005
<i>Pinus strobus</i>	Night	45	0.259	0.215	0.112	0.159	0.206
<i>Pinus strobus</i>	24 h	45	0.207	0.184	0.051	0.047	0.078
<i>Populus tremuloides</i>	Midday	246	0	0.012	0.001	0.021	0.018
<i>Populus tremuloides</i>	Day	246	0.007	0.032	0.047	0.059	0.061
<i>Populus tremuloides</i>	Night	246	0.021	0.053	0.074	0.098	0.117
<i>Populus tremuloides</i>	24 h	246	0.007	0.03	0.047	0.067	0.081
<i>Quercus macrocarpa</i>	Midday	98	0	0	0.001	0.08	0.068
<i>Quercus macrocarpa</i>	Day	98	0.013	0.025	0.158	0.192	0.185
<i>Quercus macrocarpa</i>	Night	98	0.064	0.211	0.378	0.431	0.432
<i>Quercus macrocarpa</i>	24 h	98	0.005	0.067	0.228	0.29	0.297
<i>Quercus rubra</i>	Midday	182	0.04	0.02	0.048	0.001	0
<i>Quercus rubra</i>	Day	182	0.015	0	0.014	0.03	0.027
<i>Quercus rubra</i>	Night	182	0.015	0.06	0.11	0.157	0.171
<i>Quercus rubra</i>	24 h	182	0.001	0.006	0.038	0.068	0.075

a time period for physiological adjustments to environmental temperature of both photosynthesis and respiration to occur, and that time periods of 3–6 weeks or longer might include substantial time

periods far distant from, and thus perhaps not relevant to, both the current physiological state and likely near-term future temperatures. We moreover hypothesized a simple unimodal pattern, similar for all

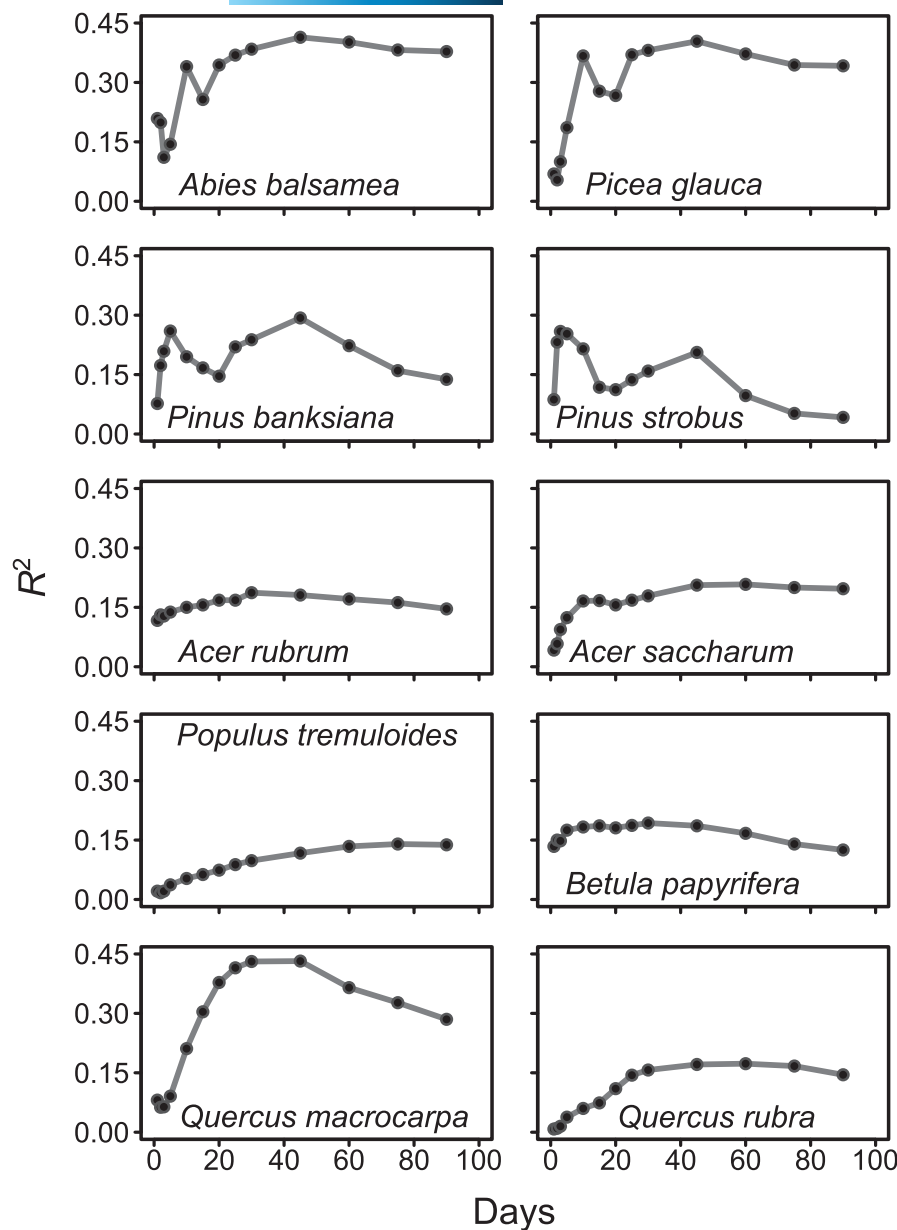


FIGURE 6 The relationship (R^2) of $\log_{10}R_{20}$ vs. average prior night temperature for differing numbers of prior nights (days) for ten species

species, where the fit of R_{20} to temperature increased as the time window increased to ≈ 10 – 15 days and then decayed as less relevant (further away in time) temperatures were included in the window. Our expectations were wrong, but not entirely so.

To our knowledge surprisingly few studies have assessed whether respiration acclimates more to daytime or nighttime temperatures. We are aware of only two published studies on the topic. In one, Will (2000) observed that R_{standard} in *Pinus taeda* needles acclimated roughly similarly to both night and day temperatures. Covey-Crump et al. (2002) observed that root respiration in *Plantago* seedlings was most strongly associated with the nighttime low temperatures. The authors speculated that effects of low temperatures might drive up sugar accumulation, and given that respiration can be related to sugar levels, might also drive up R_{standard} . Our results strongly support a greater association in all 10 species of R_{standard} with nighttime than daytime temperature,

adding considerable evidence supporting a greater impact of night than day temperatures.

Why might R_d acclimation be most closely associated with longer than shorter prior time periods? Slow acclimation in these perennial woody plants may be adaptive in light of constantly fluctuating ambient temperatures—a relatively slow acclimatory adjustment would keep plants from “chasing their own tail”—that is, avoiding repeated and costly metabolic changes and associated construction or maintenance costs—(Searle et al., 2011) as temperatures fluctuate from relatively cool to warm and back again over relatively brief periods in unpredictable patterns. It is also possible that environmental conditions, including atmospheric demand (vapor pressure deficits) and soil moisture during periods prior to measurements also influence R_d acclimation (Zhu et al., 2021) and result in better relations with longer—than shorter—prior time windows (see below for further discussion of this point).

TABLE 2 Best (and 2nd best) single term model and best overall model with more than one term, based on lowest BIC. To be selected as the best model with two or more terms a more complex model needed to be more than two units lower in AIC or BIC

Species	Best (and 2nd best) single term model				Best model with two or more terms			
	Number of nights	R^2	BIC	AIC	Number of nights	R^2	BIC	AIC
<i>Abies balsamea</i>	45 (60)	0.414	-31.2	-36.9	1, 3, 8, 15, 90	0.647	-44.0	-56.0
<i>Acer rubrum</i>	30 (45)	0.187	-228.7	-240.3	15, 25, 30	0.229	-236.4	-255.7
<i>Acer saccharum</i>	60 (45)	0.208	-144.9	-154.4	15, 20, 90	0.319	-157.7	-176.6
<i>Betula papyrifera</i>	30 (9)	0.193	-208.6	-220.1	7, 90	0.228	-218.5	-233.8
<i>Picea glauca</i>	45 (30)	0.404	0.5	-4.7	2, 8, 15, 45	0.687	-20.0	-29.5
<i>Pinus banksiana</i>	45 (5)	0.293	-52.0	-56.4	1, 5, 30, 45	0.467	-52.2	-59.8
<i>Pinus strobus</i>	8 (3)	0.272	-15.0	-19.8	8, 30, 45, 60, 75	0.697	-39.2	-48.8
<i>Populus tremuloides</i>	75 (90)	0.140	13.8	3.4	9, 45, 75	0.179	13.5	-3.8
<i>Quercus macrocarpa</i>	30 (45)	0.432	-91.6	-99.1	20, 45	0.448	-89.7	-99.6
<i>Quercus rubra</i>	60 (45)	0.173	-99.8	-109.2	75, 90	0.201	-101.0	-113.6

Moreover, if acclimation of R_d is linked in part to maintenance of photosynthetic capacity and associated with moderated variation in the realized ratio of R to net photosynthesis, we might expect that acclimation of R_d would be related to the temporal patterns and thermal sensitivity of photosynthesis (Drake et al., 2016; Wang et al., 2020; Whitehead et al., 2004). Temperature standardized V_{cmax} and light-saturated net photosynthesis were relatively stable across experimental or seasonal growth temperature variation for our study species (Bermudez et al., 2021; Reich et al., 2018; Stefanski et al., 2020), suggesting that R_d acclimation would respond principally to temperature variation that influenced realized R and A , and thus the $R:A$ ratio. Data from a study of whole-tree R_d and GPP in *Eucalyptus*, Drake et al. (2016) are consistent with this idea. That study found considerable day-to-day variation in the ratio of whole-tree $R_d:GPP$, but largely due to effects of inclement weather on GPP. Over longer integrated time periods, the $R_d:GPP$ ratio was relatively stable, except under very high temperatures.

Even in the highly seasonal and thermally variable ecotone of cold temperate and boreal forests, shifts in mean 7-day, 10-day, or 15-day moving-average temperatures of even 5°C occur relatively slowly (over weeks to months); given that the mean daily range (i.e., within 24-hour periods) of ambient aboveground temperature for our sites (May 1st–Sep 30th, 2009–2012) is $\approx 14^\circ\text{C}$, it might take several weeks for the signal-noise ratio of shifting average temperature to be sufficient as a cue for acclimation. In any case, the stronger correlation of R_{20} with night periods of 15–45 days (than short time windows) for our data is consistent with the idea that under a slowly changing mean temperature regime in a system with high intra- and inter-day variability, a long time window as a cue might be a useful strategy.

We also need to consider what processes might lead to a bimodal response of acclimation to experienced temperatures in evergreen gymnosperms, with both a recent time-window and a much longer time window correlated with acclimation. Two evergreen angiosperms in New Zealand also showed a strikingly similar bimodal

pattern as did the four evergreen conifers in our study, showing a transient peak at 3–5 days, a weaker relationship at a 20-day time window, and then increasingly stronger correlations out to a peak at 120 days (Searle et al., 2011). Neither Searle et al. (2011) nor our study has evidence to explain these dual peaks, but they are consistent with the idea that respiration includes myriad metabolic processes that operate on differing time domains and potentially with differing temperature sensitivities (Armstrong et al., 2008). Some of those myriad processes hence may be reflected in short-term (prior 3–10 nights) and/or longer-term (prior 30–45 nights) peaks in conifers (when acclimation was best associated with prior night temperatures) in our study. Among potential sources of temperature and temporal sensitivity in R_d are differences in the processes of the cytochrome c oxidase and alternative oxidase pathways (Armstrong et al., 2008).

Our results also document that different elements of the environment might influence acclimation. Models that included both prior 30-day and prior 30-night temperatures caused a shift in the relationship of R_{20} to day temperature; to a positive one (Figure S1, Tables S1 and S2), compared to the negative bivariate relationship of R_{20} to day temperature (see Figures 1 and 2). T_{night} and T_{day} are well correlated ($R > 0.75$ for the large majority of species and time windows); thus, the negative relationships of R_{20} to T_{day} alone may reflect the over-riding hidden influence of T_{night} , which likely involves the tendency to downregulate R_{20} at higher night temperatures to maintain quasi-homeostasis of realized R_d as temperatures vary (Reich et al., 2016). The positive relationship of R_{20} to $T_{30\text{ days}}$ once night temperature effects are accounted for is intriguing; so we tested whether this flip also showed up in models with both T_{night} and T_{day} for different time windows. In all 10 species at all time windows from 5 to 30 days, R_{20} was negatively related to T_{night} and positively to T_{day} ($p < .05$ for nine of ten species in all time windows).

Explanation for the positive effects of T_{day} on R_{20} could involve the impact of day temperatures on photosynthesis and thus on starch accumulation. In this ecosystem, daytime temperatures

can be relatively cool compared to the optimal for photosynthesis (Sendall et al., 2015); this is common in the morning throughout the growing season and in late spring and early fall even during the midday and afternoon. If higher photosynthesis translates into higher substrate availability for respiration, it is possible that R_{20} may upregulate (acclimate) to higher substrate levels associated with higher daytime temperatures with greater starch accumulation during the day and thus greater need for energy at night for sucrose synthesis and export (Stitt & Zeeman, 2012; Whitehead et al., 2004).

Explanation of lower R_{20} following time periods of higher daytime VPD is more difficult to explain. Although prior 30-day temperature was the dominant driver of R_{25} in tropical species (Zhu et al., 2021), R_{25} was also related to VPD, being higher at higher VPD—the opposite of what we found here. Zhu et al. (2021) speculated that higher VPD was stressful, leading to higher R_{25} associated with the repair of desiccation related cellular damage. In our study, VPD was very rarely at stressful high levels, but higher VPD was associated with lower net photosynthesis (Reich et al., 2018). It is possible that the negative association of R_{20} with VPD in our study is due to the negative impact of VPD on photosynthesis and starch accumulation, invoking the same mechanism (but opposite direction) as for daytime temperature.

Our work is also relevant to the way respiratory acclimation is quantified in ecophysiological studies and ecosystem and land surface models. Atkin et al. (2008) used the average daily (24-hour) temperature from the preceding 10 days to drive acclimation globally in the JULES model. The decision to use a 10-day average was “based on the assumption that a high degree of acclimation of R would have occurred within a 10-day period, as has been reported previously.” Several other modeling studies literally adopted the Atkin et al.'s (2008) approach and rationale in using a 10-day time window for modeling at regional to global scales (Huntingford et al., 2017; Lombardozzi et al., 2015). We are aware of one model that used a different approach—Ziehn et al. (2011) used the prior 30-day mean temperature to adjust the ratio of R_d to V_{cmax} as part of a scheme to incorporate respiratory acclimation into a process-based model. Our results suggest that although few if any other choices of time window have been used in modeling to simulate R_d acclimation, such a range of such choices should be explored.

The results of our study suggest that use of night temperature over a time window of between 30 and 45 nights would be a better choice for this set of species than using the 24-hour mean temperature for the prior 10 days (see Figure 3). For example, average correlation of R_{20} to prior 30 or 45 nights ranged from 0.24 to 0.29, versus 0.10 for correlation to 10 days (using 24-hour temperature). A 30- to 45-day period would be a reasonable choice for all 10 species, and the best choice for most species, although *P. strobus* would be best modeled using a prior 8-night period and *P. tremuloides* with a prior 60-night period. Additionally, as species on average showed near homeostasis in R_{20} when examined in relation to prior 20- to 45-night periods (Table 3), modifying ecosystem and land surface

TABLE 3 Percent acclimation averaged (means $\pm$ SE, and median) across 10 species for differing prior nighttime windows. See Results section for definition

Range of prior nights	Percent acclimation (%)	
	Mean ($\pm$ SE)	Median
0–3	68.8 $\pm$ 9.5	68.3
0–5	80.9 $\pm$ 9.5	73.7
0–10	98.5 $\pm$ 12.9	86.5
0–20	105.9 $\pm$ 10.7	87.3
0–30	116.7 $\pm$ 10.0	99.2
0–45	117.5 $\pm$ 9.6	103.7

models to account for this seems critical; especially as to our knowledge a small fraction of models simulate acclimation whatsoever and those that do neither routinely use either night temperatures or time periods longer than 10 days.

The patterns illuminated with the data in this paper help us better quantify how prior experienced temperatures, defined with differing time windows, influence R_d acclimation, and help build a foundation suggesting that night temperatures matter more than day temperatures to these processes. Such findings could help us refine model logic and associated algorithms that simulate respiratory acclimation, altering both the length of the prior time window used to drive acclimation, and which period of the 24-hour cycle to key in on. As all 17 species tested to date (10 herein, plus 7 in Will, 2000; Covey-Crump et al., 2002 and Atkin et al., personal communication) acclimate similarly or more directly to night than day or averaged 24-hour temperatures, models should adopt this approach. In addition, as all 12 species tested (10 herein, two in Searle et al., 2011) show comparable or stronger correlations with prior night temperatures at a 30- to 45-night window than a 10-night window, this also seems like a shift useful for models to take. However, species showed considerable variation in how well $R_{standard}$ related to prior night temperatures of differing time-window length, demonstrating a strong need for further quantification of such responses. Moreover, as the underlying mechanisms for the patterns observed herein—vis-à-vis acclimation of R_d to prior day vs. night temperatures expressed on different time windows—are largely unknown, bringing them to light represents an important challenge for future studies.

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AUTHORS' CONTRIBUTIONS

P.B.R., R.A.M., and R.L.R. designed the original experiment. A.S., R.L.R., and R.B. co-operated the experiment, supervised the collection and curation of the respiration data and associated leaf temperature data, as well as all experimental and ambient temperature data. P.B.R. and R.A.M. designed and coordinated the respiration measurements. A.S., K.M.S., X.W., C.Z., and J.H. conducted the respiration measurements reported herein. P.B.R. developed the idea for this study, carried out all the analyses and constructed the Figures and Tables with assistance from R.B., and wrote the first draft. All authors contributed to the interpretation of the results and to the text.

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SUPPORTING INFORMATION

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

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