A model for leaf temperature decoupling from air temperature

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ABSTRACT

Leaf temperature ($T_{leaf}$) influences rates of respiration, photosynthesis, and transpiration. The local slope of the relationship between $T_{leaf}$ and $T_{air}$, $\beta$, describes leaf thermal responses. A range of values have been observed, with $\beta < 1$ indicating limited homeothermy where $T_{leaf}$ increases at a lower rate than $T_{air}$, $\beta = 1$ indicating poikilothermy where $T_{leaf}$ tracks $T_{air}$, and $\beta > 1$ indicating megathermy where $T_{leaf}$ increasingly exceeds $T_{air}$. However, theory for variation in $\beta$ has not been developed. Here we derive an equation for $\beta$ that predicts how it varies with multiple trait and microenvironment variables. The approach also predicts how maintenance of $T_{leaf}$ away from lethally high values may help explain regulation of stomatal conductance ($g_s$). The work delineates contexts in which each class of leaf thermal response is expected and develops concepts for predicting leaf responses to thermally extreme environments.

1. Introduction

Leaf temperature, $T_{leaf}$, partially determines several ecophysiological factors that drive variation in $\beta$ is important for understanding leaf performance across environments. The value of $\beta$ may be useful for heuristic prediction of rates of photosynthesis, respiration, and transpiration in earth systems models. Additionally, the value of $\beta$ may be useful for understanding biophysical thermal effects on plant ecological strategies. Maintaining or avoiding certain temperatures may be advantageous to a plant’s growth, survival, or reproduction. For example, species in cold thermal environments might experience selection for high values of $\beta$ to increase $T_{leaf}$ relative to $T_{air}$, improving growth rates and avoiding freezing mortality, while those in warm thermal environments might experience selection for low values of $\beta$ to reduce $T_{leaf}$ relative to $T_{air}$, improving growth rates and avoiding high temperature mortality. These strategies could potentially be achieved via selection on traits influencing $\beta$ over evolutionary time.

The classes of possible leaf thermal responses can range from limited homeothermy ($\beta < 1$) (Gates, 1964; Mahan and Upchurch, 1988) in which $T_{leaf} > T_{air}$ below a certain temperature and $T_{leaf} < T_{air}$ otherwise, poikilothermy ($\beta = 1$) in which $T_{leaf} = T_{air}$ (Ansari and Loomis, 1959; Fetcher, 1981), and megathermy ($\beta > 1$) in which $T_{leaf}$ increasingly exceeds $T_{air}$ as $T_{air}$ increases (Salisbury and Spomer, 1964). All of these classes of thermal response occur in natural settings. In many cases, $\beta$ is approximately constant for a species, leading to linear $T_{leaf} - T_{air}$ relationships. However in other cases curvilinear $T_{leaf} - T_{air}$ relationships are observed, indicating that the value of $\beta$ may change...
across contexts. We present exemplar data for each class of behavior in Fig. 1, based on our original field observations of multiple co-occurring species in meadows, forests, and deserts in North America. Field methods are described in File S1 and data are provided in File S2. Additionally, in a recent global meta-analysis of leaf thermal observations (Michaletz et al., 2016), $\beta$ was commonly near 3/4 independent of the value of $T_{air}$ (i.e. limited homeothermy with no curvilinearity). However, in those data, both lower and higher values of $\beta$ also occurred, indicating that there is wide variation in leaf thermal response across species and contexts. While limited homeothermy, poikilothermy, and megathermy will have different implications for plant functioning and performance, the mechanisms that determine when each class occurs have not been fully explored.

Determining how $\beta$ varies in thermally extreme environments is also a priority for understanding plant performance in a changing climate. High $T_{leaf}$ can increase rates of respiration (Heskel et al., 2016), depress rates of photosynthesis (Doughty and Goulden, 2008; Michaletz, 2018; Slot and Winter, 2017), and increase rates of cell necrosis and leaf mortality (Bilger et al., 1984). Transpiration may sometimes be a cooling strategy to improve net carbon gain, either via avoidance of mortality (i.e. loss of all future carbon gain) or via homeostasis of temperature (i.e. maintenance near the optimal temperature for photosynthesis). Some data from temperate biomes and glasshouses support this (Drake et al., 2018; Slot and Winter, 2016; Teskey et al., 2015; von Caemmerer and Evans, 2015), as do some limited tropical field data (Schulze et al., 1973; Slot and Winter, 2016). However, when hotter environments drive high transpiration demand, intrinsic limitation of $g_s$ to a physiological maximum may drive large increases in $T_{leaf}$. Alternatively, maintenance of $T_{leaf}$ below a lethal maximum may require large increases in $g_s$. Better understanding these tradeoffs could help improve existing theory for stomatal regulation that is focused on optimizing $g_s$ to maximize carbon gain rather than to regulate $T_{leaf}$ e.g. (Medlyn et al., 2011).

There is an opportunity to obtain general insights into the factors that can influence variation in $\beta$. While direct predictions of $T_{leaf}$ are already possible from energy balance theory (Campbell and Norman, 2012; Gates, 1980; Monteith and Unsworth, 2007; Paw U, 1987), less is known about what determines rates of change in $T_{leaf}$ i.e. $\beta$. Here we derive an exact analytical solution for $\beta$ from energy balance theory. We then use this solution to predict when each class of leaf thermal response occurs, highlighting the specific environment or trait drivers underlying each scenario. We then derive additional theory for $g_s$ also based on energy balance theory, which highlights the strategies available to leaves in thermally extreme environments.

2. Methods

We begin with a classic result from energy balance theory following the notation of Monteith and Unsworth (2007). The energy budget of a leaf can be written as:

$$\varepsilon R_n \Delta T_{leaf} + R_\alpha \alpha_i = 2pc_v \left( \frac{T_{leaf} - T_{air}}{T_{air}} + \frac{mg_s(h_{air} - h_{leaf})}{\gamma + \gamma g_s T_{air}} \right)$$

(2)

A derivation of this equation is available in File S3; definitions of all parameters are given in Table 1. Further analytical progress toward $\beta$ by solving for $T_{leaf}$ and applying Eq. (1) is not immediately possible, because $T_{leaf}$ cannot be isolated as a function of $T_{air}$. This is because $T_{leaf}$ appears in polynomial terms and in nonlinear $g_s$ and $r_H$ functions, yielding an insoluble transcendental equation. While the Penman linearization allows for an approximate solution for $T_{leaf}$ (e.g. (Campbell and Norman, 2012; Monteith, 1965)), we advance without such approximations.

We now present an approach to obtain an exact explicit solution for $\beta$. The approach relies on implicit differentiation of Eq. (2), which eliminates the need to first solve for $T_{leaf}$. To begin, we assume that all parameters may vary with $T_{air}$, except for the physical constant $\sigma$ and those that do not vary substantially across the range of $T_{air}$ in which leaves can function ($\gamma, \rho, c_\rho$) or covary substantially with $T_{air}$ over the lifespan of a leaf ($n, \varepsilon, \alpha_i$). Implicit partial differentiation with respect to $T_{air}$ of Eq. (2) yields

$$\frac{\partial \varepsilon R_n \Delta T_{leaf}[T_{air}]}{\partial T_{air}} + \frac{\partial R_\alpha \alpha_i}{\partial T_{air}} = \frac{2pc_v \left( \frac{1 + \rho}{T_{air}} + \frac{mg_s(h_{air} - h_{leaf})}{\gamma + \gamma g_s T_{air}} \right)}{\frac{\partial T_{leaf}}{\partial T_{air}}}$$

(3)

This equation is linear in $\beta$, which means it can be algebraically rearranged to yield the solution:

$$\beta = \frac{\alpha_i}{\alpha_2}$$

(4)
and reduces to:

\[ \beta' = \frac{1}{\epsilon \sigma T \rho c \gamma g r T} \]

and must always be bounded between 0 and 1.

\[ \epsilon \sigma T \rho c \gamma g r T \]

decreases when ei- \[ \beta \rho c \gamma g r T \]

dependent on several physical constants, microenvironmental vari-

ables, and trait variables delineated in Table 1. Limiting cases (ex-

amples presented under limiting cases, and numerically parameterized. Additionally, computer-manipulable 

d versions of Eq. (4) are available in R language as File 

S6 (Monteith and Unsworth, 2007), this result also indicates that poikilothermy will occur for small leaves or high wind speeds. However, the

scales with the square root of the ratio of leaf size to wind speed

reach zero and poikilothermy is less likely to occur.

An alternative scenario occurs when the resistance to convective

heat transport becomes very large, i.e. for large leaves or low wind

speeds (though at low wind speeds free convection may prevent this

resistance from becoming strictly in-

fi

dependent between 0 and 1.

There are two implications that arise from this simplified for-

mula. First, the term in the numerator is always no larger than the

second term in the denominator, because \( h \) is always between 0 and 1.

The first term in the denominator is strictly positive, because all pa-

rameters are non-negative. This analysis proves that under these as-

sumptions, the value of \( \beta \) must always be bounded between 0 and 1.

That is, when variables in the energy balance are uncorrelated with

variation in \( T_{air} \), only limited homeothermy and poikilothermy are

possible. Second, \( \beta_{const} \) can be further simplified when stomatal con-

ductance is zero as

\[ \lim_{\gamma \rightarrow 0} \beta_{const} = \frac{1}{1 + \frac{\rho c y r T}{\sigma T \rho c y}} \]

Thus, when transpiration is zero or small, \( \beta_{const} \) decreases when ei-

ther \( r_H \) or \( T_{leaf} \) increases, due to nonlinearities in the relationship be-

tween radiative and convective heat transport. The overall outcome is

curvilinear in \( T_{leaf} - T_{air} \) plots.

3.2. Limiting cases with covariances

Additional insights are also possible using the full solution for \( \beta \) 

where covariances between variables are possible. First, consider the 

limiting case of a smooth approach to no resistance to convective heat 

transport, i.e. \( r_H = 0 \) and \( r_T = 0 \). In this case, 

\[ \beta = 1 \]

Thus, poikilothermy is the only scenario possible when there is no

resistance to convective heat transport, i.e. when there is full coupling 

between leaves and the atmosphere. Because \( r_H \) of isolated leaves often 

scales with the square root of the ratio of leaf size to wind speed

(Monteith and Unsworth, 2007), this result also indicates that poiki-

lothermy will occur for small leaves or high wind speeds. However, the

sheltering effect of non-isolated leaves in complex canopies

(Michalez and Johnson, 2006; Smith and Carter, 1988) means that \( r_H \) is unlikely to

reach zero and poikilothermy is less likely to occur.

An alternative scenario occurs when the resistance to convective heat transport becomes very large, i.e. for large leaves or low wind speeds (though at low wind speeds free convection may prevent this resistance from becoming strictly infinite). In this case, 

\[ \lim_{r_H \rightarrow \infty} \beta = \frac{\epsilon y S_{leaf}}{8 \sigma r_T T_{leaf}^4} \]

Table 1

Definitions of model parameters and central values used to draw example figures.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Definition</th>
<th>Parameter</th>
<th>Units</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>Stefan-Boltzmann constant</td>
<td>( \sigma )</td>
<td>W m(^{-2})K(^{-4})</td>
<td>5.67 \times 10(^{-8})</td>
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<td>Vapor pressure approximation constant</td>
<td>( \nu_0 )</td>
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<td>( \nu_1 )</td>
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<td></td>
<td>Vapor pressure approximation constant</td>
<td>( \nu_4 )</td>
<td>K</td>
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<tr>
<td></td>
<td>Psychrometer constant</td>
<td>( \gamma )</td>
<td>Pa K(^{-1})</td>
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</tr>
<tr>
<td></td>
<td>Heat capacity of air</td>
<td>( cp )</td>
<td>J g(^{-1})K(^{-1})</td>
<td>1.01</td>
</tr>
</tbody>
</table>

| Micro-environment | Air temperature                             | \( T_{air} \) | K              | 90             |
|                  | Leaf temperature                            | \( T_{leaf} \) | K              | 293            |
|                  | Relative humidity                            | \( h \)     | –              | 0.5            |
|                  | Vapor pressure                              | \( \epsilon \) | Pa             | –              |
|                  | Wind speed                                  | \( u \)     | m s\(^{-1}\)   | 1              |
|                  | Incident longwave radiation                 | \( r_l \)   | W m\(^{-2}\)  | 400            |
|                  | Incident shortwave radiation                | \( r_s \)   | W m\(^{-2}\)  | 800            |
| Trait            | Emissivity                                   | \( \epsilon \) | –              | 0.97           |
|                  | Absorbance (shortwave)                      | \( \alpha \) | –              | 0.5            |
|                  | Convective resistance                       | \( r_H \)   | m s\(^{-1}\)   | 100            |
|                  | Stomatal conductance                         | \( g_S \)   | m s\(^{-1}\)   | 0.005          |
|                  | Stomatal ratio                               | \( n \)     | –              | 1              |

\[ \omega_1 = -\frac{1}{g y S_{leaf}^3 (1 + g y S_{leaf} r_H T_{leaf})^2} 2 \sigma y r_H \epsilon S_{leaf} T_{leaf} (1 + g y S_{leaf} r_H T_{leaf}) (\gamma + \epsilon S_{leaf} h T_{leaf}) + \epsilon \sigma y S_{leaf} T_{leaf} (1) \]

\[ \omega_2 = 8 \epsilon \sigma y S_{leaf}^3 + 2 \sigma y r_H \epsilon S_{leaf} T_{leaf} (1 + g y S_{leaf} r_H T_{leaf}) \]

Eq. (4) can now be manipulated, simplified under limiting cases, and numerically parameterized. Additionally, computer-manipulable

d versions of Eq. (4) are available in R language as File 

S4 and File S5, and a numerical version of Eq. (4) is available in Mathematica language as File S4 and File S6.

3. Results

Conceptual insights into the drivers of \( \beta \) can be obtained by ex-

aimining limiting cases of Eq. (4), by exploring covariance among

variables, and by making numerical simulations. The exact solution for

\( \beta \) depended on several physical constants, microenvironmental vari-

ables, and trait variables delineated in Table 1. Limiting cases (ex-

ploring the consequences of taking certain variables to zero or infinite

values) provide an approach to explore the effects of biologically ‘small’ and ‘large’ values of each variable. These analyses involve starting with a minimal set of covariances between model variables and \( T_{air} \), then adding additional covariances in order to model increasingly realistic phenomena.

3.1. Limiting cases without covariances

First, in a simple case assuming no covariance between model

variables and \( T_{air} \) (except for the saturation vapor pressure of air and thus the vapor pressure deficit, which must change due to physical

phase changes), the solution for \( \beta \) becomes \( \beta_{const} \) and reduces to:

\[ \beta_{const} = \frac{\epsilon y S_{leaf} (1 + g y S_{leaf} r_H T_{leaf}) + \epsilon \sigma y r_H \epsilon S_{leaf} T_{leaf}}{4 \epsilon \sigma y r_H \epsilon S_{leaf} T_{leaf} (1 + g y S_{leaf} r_H T_{leaf})} \]

There are two implications that arise from this simplified formulation. First, the term in the numerator is always no larger than the

second term in the denominator, because \( h \) is always between 0 and 1. The first term in the denominator is strictly positive, because all pa-

rameters are non-negative. This analysis proves that under these as-

sumptions, the value of \( \beta \) must always be bounded between 0 and 1.
This equation demonstrates that \( \beta \) decreases with increasing \( T_{\text{leaf}} \) and increases when either \( R_l \) or \( R_s \) positively co-varies with \( T_{\text{air}} \). Some positive co-variance between \( R_l \) and \( T_{\text{air}} \) is likely due to heat transfer between air and ground leading to correlations between air and ground temperatures. Additionally, the numerator of Eq. (10) is potentially unbounded, with the numerator exceeding the denominator when \( \varepsilon R_l [T_{\text{air}}] + \alpha R_s [T_{\text{air}}] > 8 \sigma^2 T_{\text{leaf}}^4 \). Thus megathermy can occur when air temperatures and incident solar radiation are simultaneously high.

A similar finding also occurs when stomatal conductance drops smoothly to zero:

\[
\lim_{T_{\text{leaf}} \to 0,0 < \beta < 1} \beta = \frac{2\sigma T_{\text{leaf}}^3 + (1 + T_{\text{leaf}}) \varepsilon R_l [T_{\text{air}}] + \alpha R_s [T_{\text{air}}]}{2\sigma T_{\text{leaf}}[\rho c^2 T_{\text{leaf}}^3 + 4 \sigma^2 T_{\text{leaf}}^3 R_l [T_{\text{air}}]]}
\]

(11)

This equation remains complex, but under the further assumption that \( T_{\text{leaf}} \) simultaneously tends towards becoming independent of \( T_{\text{air}} \) (reasonable unless wind speed or leaf size varies with \( T_{\text{air}} \), e.g. for species that close/move their leaves in high heat (Ehleringer and Forseth, 1980) or that evolve smaller leaves in hot and arid environments (Wright et al., 2017)), this further reduces to

\[
\lim_{T_{\text{leaf}} \to 0,0 < \beta < 1} \beta = \frac{2\sigma T_{\text{leaf}}^3 + (1 + T_{\text{leaf}}) \varepsilon R_l [T_{\text{air}}] + \alpha R_s [T_{\text{air}}]}{2\sigma T_{\text{leaf}}[\rho c^2 T_{\text{leaf}}^3 + 8 \sigma^2 T_{\text{leaf}}^3 R_l [T_{\text{air}}]]}
\]

(12)

In this case, the numerator exceeds the denominator when \( 8 \sigma^2 T_{\text{leaf}}^4 \beta < \varepsilon R_l [T_{\text{air}}] + \alpha R_s [T_{\text{air}}] \). Thus megathermy can occur if there is a positive co-variance between \( R_l \) or \( R_s \) and \( T_{\text{air}} \) and either convective resistance is sufficiently high or stomatal conductance is sufficiently low.

Under the alternative scenario that the stomatal conductance becomes very large and the convective resistance becomes zero,

\[
\lim_{T_{\text{leaf}} \to 0,0 < \beta < 1} \beta = \frac{\gamma + n R_l [T_{\text{air}}] h [T_{\text{air}}] + n h [T_{\text{air}}] \varepsilon [T_{\text{air}}]}{\gamma + n R_l [T_{\text{air}}]}
\]

(13)

Because \( e_i \) is a monotonic concave increasing function of \( T_{\text{air}} \), \( e_i [T_{\text{air}}] < e_i [T_{\text{leaf}}] \) if and only if \( T_{\text{air}} < T_{\text{leaf}} \). Thus the first two terms of the numerator divided by the denominator always will be less than one if \( T_{\text{air}} < T_{\text{leaf}} \), and may be less than one depending on \( h \). Thus limited homeothermy is the likely outcome when stomatal conductance is high and convective resistance is low.

When \( h \) increases with \( T_{\text{air}} \) (i.e. warmer conditions are also relatively wetter), then the third term of Eq. (13) is positive; if this increase is sufficiently large, then the numerator of this equation can exceed the denominator, leading to \( \beta > 1 \) and megathermy. Alternatively if \( h \) negatively co-varies with \( T_{\text{air}} \) (i.e. warmer conditions are also relatively drier), then the third term in the numerator is negative. If it becomes sufficiently negative, then the overall numerator can become negative, leading to \( \beta < 0 \). We are unaware of any empirical evidence for declines in \( T_{\text{leaf}} \) with increases in \( T_{\text{air}} \), but it is a theoretical possibility.

3.3. Numerical predictions

To test our predictions for \( \beta \), we also plot predictions of Eq. (4) as a function of several independent variables. Predictions are for a leaf described by the central parameter values and ranges in Table 1, with one or two parameters varying across a biologically broad range, either independently or with certain covariances with \( T_{\text{air}} \). The central parameter values represent a medium-sized hypostomatous leaf in midday sun with light wind. To make numeric predictions, we specify the form of the saturation vapor pressure of water using the Arden-Buck equation (Buck, 1996):

\[
\varepsilon_3(T) = v_3 \exp \left( \frac{(T - v_3)}{v_4} \right) \left( \frac{T - v_1}{v_4 + (T - v_2)} \right)
\]

(14)

where \( v_1 - v_4 \) are constants (Table 1).

To illustrate some predictions of Eq. (4), we next consider two example cases where model parameters vary with \( T_{\text{air}} \). In the first case, we explore how variation in \( \beta \) arises from variation in the strengths of covariation between stomatal conductance and \( T_{\text{air}} \) (\( g_s \) and \( T_{\text{air}} \)) and shortwave radiation and \( T_{\text{air}} \) (\( R_l \) and \( T_{\text{air}} \)), with all other parameters set to constant central values (Fig. 2A). In this case, when covariation in either parameter is strongly positive, \( \beta \) can take values above or below 1, consistent with the above analysis and reflecting the contrasting influences of shortwave radiation and transpiration in heating and cooling the leaf. In the second case, we explore how predictions for \( \beta \) vary as a function of changes in leaf traits when non-zero covariances between stomatal conductance and \( T_{\text{air}} \) and shortwave radiation and \( T_{\text{air}} \) are incorporated (Fig. 2B). When setting \( g_s \) (\( T_{\text{air}} \)) = -0.0002 m s\(^{-1}\) K\(^{-1}\) and \( R_l \) (\( T_{\text{air}} \)) = 30 W m\(^{-2}\) K\(^{-1}\), and allowing the albedo \( \alpha \) and the convective resistance \( r_c \) to vary, we also find that values of \( \beta \) can be consistent with all classes of leaf thermal response. While Fig. 2 illustrates only two of many possible examples, it demonstrates that the covariance between model parameters and \( T_{\text{air}} \) is central to influencing the realized values of \( \beta \). The code provided in File S4 can be used to explore other scenarios.

3.4. An approximate solution for \( g_s \)

The above theory has highlighted the critical role of stomatal conductance in modulating \( T_{\text{leaf}} \) in different microclimates and for leaves with different traits. To better understand these tradeoffs, we also obtain an approximate solution for \( g_s \) based on energy balance theory. The full energy balance (Eq. (2)) can be algebraically re-arranged to yield

\[
g_s = \frac{\gamma(2\sigma T_{\text{air}} - T_{\text{leaf}}) + n(2\sigma T_{\text{leaf}} - R_l - R_s)}{n(\gamma R_l - 2\sigma^2 T_{\text{leaf}}^4 + \gamma T_{\text{leaf}} + n R_l [T_{\text{air}}] - n h [T_{\text{air}}])}
\]

(15)

This equation describes the value of \( g_s \) that must be obtained to balance the energy budget for a given value of \( T_{\text{leaf}} \) and \( T_{\text{air}} \). This equation has solutions that can range from \(-\infty\) to \(+\infty\), but this full range is not physiologically relevant. We therefore next solve for the \( T_{\text{leaf}} \) values under which \( g_s \) is positive and finite.

The minimum value of \( g_s \) is zero. This value is obtained when the numerator of Eq. (15) is zero, a constraint that simplifies to

\[
T_{\text{air}} = T_{\text{leaf}} - \frac{R_l}{2\sigma T_{\text{leaf}}^3}(\varepsilon R_l + \alpha R_s - 2\sigma T_{\text{leaf}}^4)
\]

(16)

This equation describes a curve through the \( T_{\text{air}}-T_{\text{leaf}} \) plane whose intercept decreases with increasing incident radiation and whose positive curvature and intercept increases with increasing \( T_{\text{leaf}} \). This curve is above the 1:1 line if the outgoing blackbody radiation exceeds the incident radiation and below it otherwise.

The maximum value of \( g_s \) is \(+\infty\). This value is obtained when the denominator of Eq. (15) is zero, a constraint that simplifies to

\[
\gamma R_l - 2\sigma^2 T_{\text{leaf}}^4 + \gamma T_{\text{leaf}} + n R_l [T_{\text{air}}] - n h [T_{\text{air}}] = 0
\]

(17)

This equation can be further simplified by assuming that \( T_{\text{leaf}} \) takes a value close to \( T_{\text{air}} \). After a first-order Taylor series expansion of \( T_{\text{air}} \) around \( T_{\text{leaf}} \), assuming reasonably that only \( g_s \) varies with \( T_{\text{leaf}} \), an equation can be found as:

\[
T_{\text{air}} = \frac{-\gamma R_l - \alpha R_s - 2\sigma^2 T_{\text{leaf}}^4 + \gamma T_{\text{leaf}} + n R_l [T_{\text{air}}] - n h [T_{\text{air}}]}{2\sigma^2\gamma + n h [T_{\text{air}}]}
\]

(18)

This equation now describes a unique curve in the \( T_{\text{air}}-T_{\text{leaf}} \) plane. In the case of \( h = 0 \), it can be interpreted as an offset from the 1:1 line where increasing radiation lowers the intercept, and increasing \( T_{\text{leaf}} \) increases the positive curvature and intercept.

The set of \( T_{\text{leaf}} \) and \( T_{\text{air}} \) values between the curves described by Eqs. (16) and (18) represents the possible thermal operating space for a leaf. However, this operating space is further constrained in two additional
ways. First, the asymptote described by Eq. (18) represents $g_S = +\infty$. However, a more realistic limit would be set by a value $g_{S,max}$ that describes the physiological maximum stomatal conductance of the leaf. Such a limit would yield another curve intermediate to Eqs. (16) and (18), further restricting the thermal operating space.

Additionally, there are further constraints set by $T_{leaf} < T_{stress}$ and $T_{leaf} < T_{lethal}$, where $T_{stress}$ and $T_{lethal}$ are temperatures at which thermal stress (often near 35 °C; Doughty and Goulden, 2008; Michaletz, 2018; Slot and Winter, 2017) and mortality (often near 45 °C; O’Sullivan et al., 2017), respectively, would occur. These two additional constraints lead to a wedge-shaped band of feasible $T_{air}$ and $T_{leaf}$ values. To illustrate this restricted thermal operating space, we also plot numerical predictions for $g_S$ based on Eq. (15) using the central parameter values in Table 1. The multiple constraints described above are evident in Fig. 3, leaving a narrow band of

Fig. 2. Example predictions for variation in the slope $\beta$ of the $T_{leaf} - T_{air}$ relationship. Contour plots are colored redder if $\beta > 1$, gray if $\beta = 1$, and bluer if $\beta < 1$. Predictions arise from Equation M-13 using central values in Table 1, except for the parameters that are varied in each panel. A) Variation in $\beta$ due to changes in the strengths of covariation between $T_{air}$ and $g_S$, or between $T_{air}$ with $R_s$. B) Variation in $\beta$ due to changes in the convective resistance, $r_H$, and the albedo, $\alpha$, assuming covariances of $g_T (T_{air}) = -0.0002 \text{ m s}^{-1} \text{ K}^{-1}$ and $R_s (T_{air}) = 30 \text{ W m}^{-2} \text{ K}^{-1}$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 3. Example predictions for stomatal conductance, $g_S$, as a function of $T_{leaf}$ and $T_{air}$, with all non-focal parameters set to constant values in Table 1 except a positive covariance between air temperature and solar radiation: $R_l = R_s = 500 + (10(T_{air}) - 273)$, corresponding to a linear increase from 500 W m$^{-2}$ at 0 °C to 1000 W m$^{-2}$ at 50 °C. Only a restricted range of $T_{leaf}$ and $T_{air}$ combinations yield a positive value of $g_S$ (black-green-yellow shading). Values of $g_S$ above an example physiological maximum conductance $g_{S,max}$ are shown in purple and indicate mathematically possible but physiologically impossible values. Values of $T_{leaf}$ above a value causing stress or mortality ($T_{stress}$ and $T_{lethal}$, here illustrated at 35 °C and 45 °C respectively) are shown in orange and red. The 1:1 line is shown in white. There is a restricted feasible thermal operating space corresponding to conditions not shaded in orange, red, or purple, and a limited amount of latitude for varying $T_{leaf}$ given $T_{air}$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
4. Discussion

4.1. Implications for leaf thermal response

Our main result is a conceptual clarification of the environmental and trait contexts in which each class of leaf thermal response occurs. Limited homeothermy ($\beta < 1$) is predicted when energy balance parameters are constant with respect to $T_{air}$ (probably unrealistic) or when stomatal conductance is high and convective resistance is low (more realistic). Poikilothermy ($\beta = 1$) occurs when convective resistance is low. Megathermy can occur when microclimate or trait parameters co-vary in certain ways with $T_{air}$, e.g. when incident radiation or relative humidity increase with $T_{air}$. These results are valid under the limiting scenarios explored, but the nonlinearities in Eq. (4) also indicate that the relationships are not one-to-one. A wider range of mappings between parameters and $\beta$ values are also possible (e.g. poikilothermy may also occur for other parameter combinations that do not include low convective resistance).

Our results are important for conceptually delineating when and how $T_{air}$ is decoupled from $T_{leaf}$ with subsequent implications for predicting carbon/water fluxes or leaf mortality that are temperature-dependent. We showed that accounting for covariance between energy balance parameters and $T_{air}$ is critical for accurately predicting leaf thermal response. These covariances may be set by physical or biological processes and are relevant at timescales ranging from within the lifespan of a leaf to the evolution of a clade. Our work helps identify the impact of each type of covariance on leaf thermal response. For example, within the lifespan of a leaf, if increased $T_{air}$ leads to turgor-induced decreases in leaf angle (Fu and Ehleringer, 1989), then $R_s$ will also decrease, leading to reductions in $\beta$. Alternatively, over evolutionary timescales, if leaf size negatively covaries with $T_{air}$ (Ehleringer and Forse, 1986; Wright et al., 2017), then $R_s$ will decrease with $T_{air}$, and $\beta$ will decrease. Additionally, environmental variables are nominally externally controlled and set the context for the leaf’s thermal response, while the trait variables are nominally under the control of the organism and can modulate the leaf’s thermal response, either over the lifespan of a single leaf (e.g. by varying $g_{s}$) or over ecological timescales (e.g. through leaf plasticity) or over evolutionary timescales (e.g. adaptation of new phenotypes). Organisms may also indirectly modulate their microenvironment at all of these timescales by changing other traits not included in Table 1. For example, changes in branch angle or canopy openness (e.g. via changes in leaf area index) could influence $R_s$ or $R_t$. Thus, many factors may allow for selection on $\beta$, or alternatively, selection on these factors may indirectly cause variation in $\beta$.

Our modeling results show that values of $\beta$ can range from below 1 to above 1, whereas the majority of reported data (Dong et al., 2017; Drake et al., 2018; Michaletz et al., 2016; Yu et al., 2015) are consistent with $\beta < 1$. This mismatch requires further exploration. We suggest that because these empirical data primarily came from previously published leaf ecophysiology studies, they are biased towards observations of isolated leaves under optimal conditions for photosynthesis, i.e. the low $R_t$, high $g_{s}$ conditions that are predicted to yield limited homeothermy. When water is limiting, stomatal conductance is low, and carbon assimilation is low (which corresponds also to realistic conditions that may not be optimal for photosynthesis, including parameter covariances with $T_{leaf}$), energy balance theory instead

predicts megathermy. Some reported data have exhibited megathermy (Lin et al., 2017; Salisbury and Spomer, 1964), although such reports are few relative to those for limited homeothermy. Our original datasets (Fig. 1) are also consistent with a wide range of values of $\beta$ occurring in nature. Nevertheless, they are also insufficient to formally test the predictions of our model. Comparing observed and predicted values of $\beta$ would require simultaneous measurements of multiple micro-environment variables (Table 1), as in extant formal tests of extant energy budget theory. Thus, prioritizing observations of $T_{leaf}$ in other environmental and physiological conditions and for more extreme leaf forms may lead to wider appreciation of the breadth and prevalence of thermal responses that are possible.

4.2. Implications for stomatal regulation

Our analysis of $g_{s}$ in an energy balance context also highlighted the conceptual importance of thermal ecology in regulating stomatal behavior. Variation in $\beta$ is likely to be critical for this coordination by either amplifying or damping changes in $T_{leaf}$ as $T_{air}$ varies externally. The water costs of maintaining a given leaf for a projected range of future environmental conditions probably must be traded off against the potential benefits of instead abandoning the leaf, conserving the water, and spending the water on maintaining a different leaf at a later time in different thermal environments (Sperry et al., 2016; Wolf et al., 2016). In a few limited cases, data do suggest that high transpiration can occur without photosynthesis when $T_{air}$ is high (Drake et al., 2018; Schulze et al., 1973; Slot and Winter, 2016; Teskey et al., 2015; von Caemmerer and Evans, 2015), but it is unclear how general these results are.

We (and recently others (Drake et al., 2018)) hypothesize that in environments with high $T_{air}$, leaves may sometimes spend water (i.e. increase $g_{s}$, or at least decrease $g_{s}$ less than predicted by classic stomatal regulation models (Medlyn et al., 2011)) in order to avoid mortality and retain the possibility of future carbon gain (Ball et al., 1988; Parkinson and Louches, 1972). We predict that this phenomenon would be more likely for species with costly or long-lived leaves where water is readily available, where the sunk costs or potential future carbon gain is high, or in environments where rapidly drawing down shared water resources produces a competitive advantage (Wolf et al., 2016), e.g. sun-exposed tropical forest canopies experiencing high annual precipitation (Ball et al., 1988). However, we also predict that when water is not readily available (e.g. hot deserts), $g_{s}$ may not be regulated to limit high values of $T_{leaf}$ because conditions under which cooling would be advantageous are those where water is scarcest.

This hypothesis implies that leaves are shed when the water costs of avoiding thermal mortality exceed the carbon benefits of retaining a leaf. There is thus an opportunity to extend contemporary stomatal models which primarily focus on maximizing performance by maximizing carbon gain per unit water lost (Cowan and Farquhar, 1977), maximizing carbon profit (Sperry et al., 2016) or optimizing competition for water and avoiding hydraulic impairment (Wolf et al., 2016). These models could instead consider additional optimization criteria related to avoidance of thermal mortality, as informed by the limits identified in e.g. Fig. 3. Additionally, better data from thermally extreme environments are needed to assess whether this alternate stomatal behavior is common. Such work could improve prediction of plant water loss and carbon gain in thermally extreme environments that may become increasingly prevalent under global change (Grossiord et al., 2017; Sevanto and Xu, 2016).

Competing interests

We have no competing interests.
Author contributions

BB developed theory with input from SM. BB and SM collected data. BB and SM wrote the manuscript. SM was supported by a Los Alamos National Laboratory Director’s Fellowship.

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Appendix A. Supplementary data

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References