

## Opinion

## Plant Thermoregulation: Energetics, Trait–Environment Interactions, and Carbon Economics

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**Building a more predictive trait-based ecology requires mechanistic theory based on first principles. We present a general theoretical approach to link traits and climate. We use plant leaves to show how energy budgets (i) provide a foundation for understanding thermoregulation, (ii) explain mechanisms driving trait variation across environmental gradients, and (iii) guide selection on functional traits via carbon economics. Although plants are often considered to be poikilotherms, the data suggest that they are instead limited homeotherms. Leaf functional traits that promote limited homeothermy are adaptive because homeothermy maximizes instantaneous and lifetime carbon gain. This theory provides a process-based foundation for trait–climate analyses and shows that future studies should consider plant (not only air) temperatures.**

## Plant Thermoregulation: Implications for Plant Functioning

Many plants can thermoregulate to maintain relatively stable tissue temperatures in the face of variable environmental temperatures [1–5]. Some use variation in leaf functional traits to passively thermoregulate and avoid unfavorable temperature extremes [6–8]. Others create metabolic heat to actively thermoregulate and attract pollinators or increase growth rates [9]. Despite this diverse and scattered literature, the implications of thermoregulation have been difficult to implement. Many studies in physiology, ecology, and climate science still regard plants as poikilotherms – with temperatures that are determined solely by the environment [4]. As a result, it is commonly assumed that plant temperatures are equal to the ambient air temperature [10].

We focus hereon an important outcome of thermoregulation that has potential to unite trait-based ecology: limited homeothermy. Because it weakens the links between climate and plant performance [4,11,12], limited homeothermy has implications for how we model trait–climate interactions, plant growth rates, vegetation dynamics, and the carbon budgets of ecosystems. Using the example of plant leaves, we explore how the interplay of morphology and physiology leads to limited homeothermy.

## The Limited Leaf Homeothermy Hypothesis

The limited leaf homeothermy hypothesis (cf. [4]) posits that specific suites of leaf traits have evolved via natural selection to buffer variation in environmental temperature and maintain leaf temperatures within a narrower range of variation around metabolic optima. It predicts that leaf

## Trends

Plants are generally considered to be poikilotherms that do not thermoregulate. However, empirical data show that plants are actually limited homeotherms that do thermoregulate.

Plant thermoregulation and limited homeothermy decouples physiological functioning from climatic variation to promote metabolic homeostasis and maximize carbon assimilation and fitness.

Energy budgets and carbon economics provide a mechanistic theory for understanding and predicting these relationships. Specifically, theory suggests that thermoregulation evolved via natural selection on traits to maximize lifetime carbon gain, growth, production, and fitness across climate gradients.

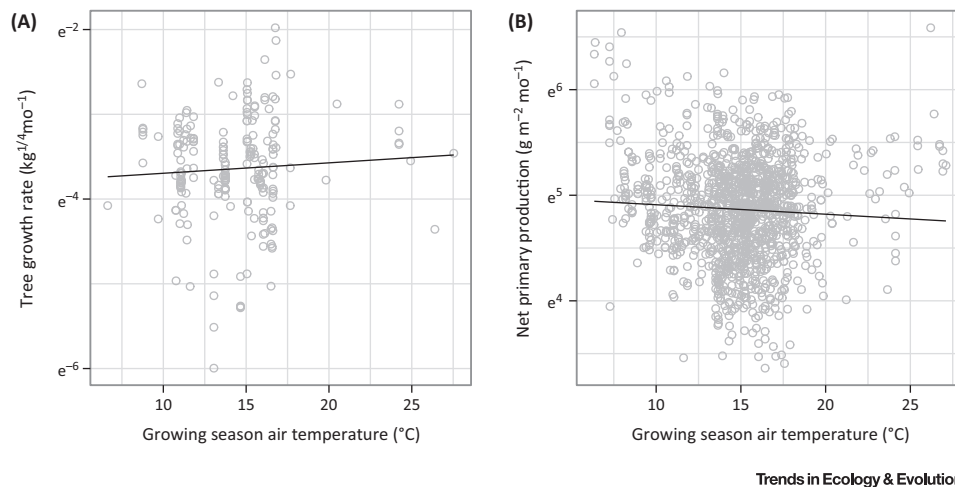
Future studies need to consider plant tissue (and not only air) temperatures.

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**Figure 1. Global Invariance of Plant Growth and Forest Production across Air Temperature Gradients.** (A) Mass-corrected monthly ( $\text{mo}^{-1}$ ) tree growth rate does not vary with air temperature ( $P = 0.365$ ,  $r^2 = 0.004$ ). Figure redrawn from [19]. (B) Monthly net primary production varies marginally with air temperature ( $P = 0.048$ ), but none of the variation is explained by air temperature ( $r^2 = 0.003$ ). Figure redrawn from [20].

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temperatures are controlled passively via coordinated shifts in climate, functional traits, and leaf physiology. The hypothesis assumes that limited homeothermy is advantageous because it allows, in the face of wide variation in ambient air temperatures, the continuous use of a common set of photosynthetic and respiration enzymes with relatively narrow thermal tolerance ranges, and/or stabilizing metabolic reaction rates to maintain positive carbon balance. The end result is a maximization of net carbon assimilation, growth, production, and fitness across climate gradients (Figure 1). If correct, this photosynthesis-weighted view of leaf homeothermy will reshape our understanding of plant–climate interactions, with profound implications for studies in plant and ecosystem ecology that commonly use air temperature as a proxy for plant temperature [10].

### Leaf Energetics Unifies Our View of Thermoregulation and Trait–Climate Interactions

Although leaf energy balance and photosynthesis are deeply interwoven, they are often considered in isolation (cf. [13]). This separation reflects a logistical legacy because measuring photosynthesis via modern field methods necessarily removes a leaf from its natural environment, and measuring the natural energy balance of a leaf precludes measurements of photosynthesis. However, plants are photoautotrophic, sessile organisms. The solar radiation they use to synthesize chemical energy also affects the temperatures of their leaves.

Although it has been known for more than a century that temperature influences physiological and metabolic rates [14], predicting how climate affects organismal performance is more complicated, given the decoupling of plant and air temperatures. Temperature has strong and well-documented effects on tissue-level rates of metabolism [15] and physiology [16]. Even so, recent studies have shown that tissue-level results do not scale up to individuals and ecosystems. For example, air temperature is a poor predictor of plant growth and production after controlling for standing biomass, plant age, and growing season length (Figure 1) [17–20]. Clearly, our understanding of how climate influences plant physiology and performance remains incomplete, and a more mechanistic approach is needed [21,22].

The trait-based approach, heralded as a new paradigm in ecology [13,23], shows considerable promise. The approach posits that functional traits mediate organism–environment interactions,

and consequently reflect differences in ecological strategies, performance, and fitness [24,25]. Thus, traits can vary across climatic gradients [26–30] as a result of environmental filtering and niche partitioning [31]. While trait-based ecology has made substantial progress in characterizing trait–environment relationships [22,30,32,33], it lacks a firm mechanistic foundation [34,35] and is still primarily correlation-based [22,32,33].

Energy budgets provide a powerful process-based approach for linking climate, functional traits, and physiological performance. They have a long history of development and use in physiology, thermal ecology, and ecosystem ecology. They are increasingly important in animal ecology [36–41] and are seeing a resurgence in plant ecology and macroecology [7,8,42,43]. However, rarely have they been used in trait-based ecology [7,8]. Such process-based theory is necessary to understand and predict trait–climate relationships.

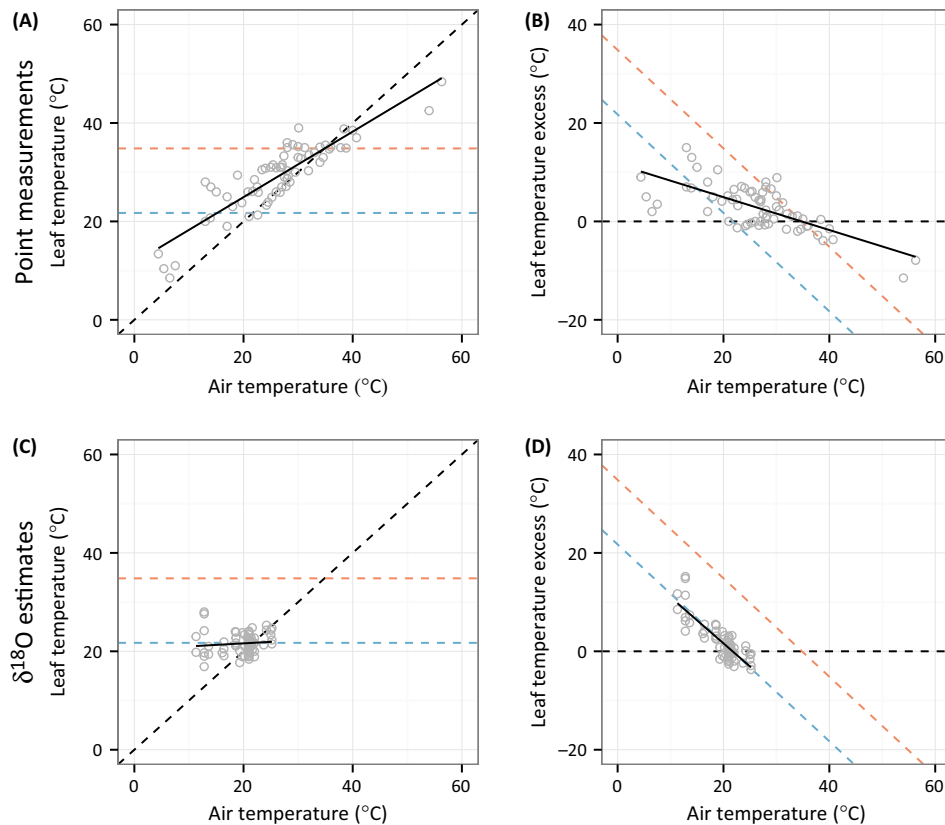
In the coming sections we evaluate evidence for the limited homeothermy hypothesis by assessing variation in leaf temperature, plant growth, and ecosystem productivity across global climate gradients. We review and apply energy budgets to link co-variation in climate and leaf traits to temporal average and dynamic leaf temperatures. Finally, we outline theory and predictions for relationships between key leaf functional traits, leaf temperature dynamics, and leaf carbon economics.

### Evaluating the Limited Leaf Homeothermy Hypothesis

The limited homeothermy hypothesis is based on a long history of theory and observation [1,2,4,5,11,44–47]. We review here some of the empirical support for the hypothesis, using leaf and air temperature data estimated by two different approaches.

The first approach ignores photosynthetic physiology and examines short-term point measurements of leaf temperature across a large air temperature gradient. Data for 68 leaves from over 62 species spanning an air temperature gradient of  $\sim 50^{\circ}\text{C}$  are plotted in Figure 2A,B [1]. Ordinary least squares regression showed that leaf temperatures were  $\sim 10^{\circ}\text{C}$  warmer at air temperatures of  $5^{\circ}\text{C}$ ,  $7^{\circ}\text{C}$  cooler at air temperatures of  $55^{\circ}\text{C}$ , and conformed to air temperatures at  $35^{\circ}\text{C}$ . This supports a limited homeothermy of leaves, because the slope of 0.670 ( $r^2 = 0.822$ ; Figure 2A) is significantly greater than 0 ( $P < 2.2 \times 10^{-16}$ ) as required for true homeothermy and significantly less than 1 ( $P < 2.286 \times 10^{-12}$ ) as required for leaf–air temperature equivalence. However, a limitation of these data is that they might have been measured without regard for the physiological status of the leaf (e.g., whether or not the leaf is at peak photosynthesis).

The second approach provides a long-term photosynthetically weighted estimate of whole-crown leaf temperature, which is thought to more accurately reflect average leaf temperatures when most photosynthesis takes place. Data for over 38 tree species are plotted in Figure 2C,D [11]. Here, leaf temperatures were estimated using a cellulose  $\delta^{18}\text{O}$  model [48] parameterized with data for climate and wood cellulose  $\delta^{18}\text{O}$  [11]. Unlike the point measurements (Figure 2A,B), these  $\delta^{18}\text{O}$  estimates provide an integrated measure of variation in leaf biophysics (energy balance and biochemistry) because they quantify the ‘effective temperature’ driving rates of leaf-level metabolism and physiology. Compared to the point measurements,  $\delta^{18}\text{O}$  leaf temperatures show a still more striking temperature difference between leaf and ambient air temperatures: leaves were  $\sim 11^{\circ}\text{C}$  warmer at air temperatures of  $10^{\circ}\text{C}$ ,  $3^{\circ}\text{C}$  cooler at air temperatures of  $25^{\circ}\text{C}$ , and approximately equal at air temperatures of  $22^{\circ}\text{C}$ . This supports a photosynthetically-weighted true homeothermy of leaves because the fitted slope of 0.062 ( $r^2 = 0.010$ ; Figure 2C) is not different from 0 ( $P = 0.404$ ) and is less than 1 ( $P < 2.2 \times 10^{-16}$ ). The leaf–air temperature equivalence was lower than for point measurements, because the  $\delta^{18}\text{O}$  approach integrates leaf temperature across all leaves in a plant



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**Figure 2. Empirical Support for the Leaf Homeothermy Hypothesis.** Leaf temperatures estimated using two independent approaches support leaf homeothermy across large air temperature gradients. (A) Leaf temperature and (B) leaf temperature excess ( $T_l - T_a$ ) from short-term point measurements of 68 individual leaves from over 62 species. Figures redrawn from [1]. For leaf temperature, the fitted slope of 0.670 ( $r^2 = 0.822$ ) is greater than 0 ( $P < 2.2 \times 10^{-16}$ ) and less than 1 ( $P = 2.286 \times 10^{-12}$ ). For leaf temperature excess, the fitted slope of  $-0.330$  ( $r^2 = 0.528$ ) is less than 0 ( $P = 2.29 \times 10^{-12}$ ) and greater than  $-1$  ( $P < 2 \times 10^{-16}$ ). (C) Leaf temperature and (D) leaf temperature excess ( $T_l - T_a$ ) from long-term photosynthetically-weighted estimates from cellulosic  $\delta^{18}\text{O}$  from over 38 species of trees. Figures redrawn from [11]. For  $\delta^{18}\text{O}$  leaf temperature, the fitted slope of 0.062 ( $r^2 = 0.010$ ) is not different from 0 ( $P = 0.404$ ) and is less than 1 ( $P < 2.2 \times 10^{-16}$ ). For leaf temperature excess, the fitted slope of  $-0.938$  ( $r^2 = 0.706$ ) is less than 0 ( $P < 2 \times 10^{-16}$ ) and not different from  $-1$  ( $P = 0.404$ ). Black unbroken lines are ordinary least squares regressions, black broken lines indicate leaf-air temperature equivalence ( $T_l = T_a$ ), blue broken lines indicate a 21.72°C homeothermy, and red broken lines indicate a 34.83°C homeothermy (homeothermy isolines are leaf-air equivalence temperatures of point and  $\delta^{18}\text{O}$  temperature data, respectively).

(shaded and unshaded) whereas the point data are from sunlit leaves only. We note that while the  $\delta^{18}\text{O}$  approach to leaf temperature has been contentious [49,50], this pattern of homeothermy is consistent with that observed for point temperature data (Figure 2A–D).

These short- and long-term data show that while leaf temperature can vary substantially from air temperature (up to 29°C difference [51]), leaf temperature excess (leaf minus air temperature  $T_l - T_a$ ) is generally less than 12°C (Figure 2A–D). However, given the nonlinearities of enzyme kinetics, such temperature differences can have profound effects on plant growth and production [16,52–54], a point we return to later. Recent work has also demonstrated a limited homeothermy of apical bud meristems [12], which influences key metabolic processes that govern leaf initiation rates, plant architecture, leaf area, and growth.

**Box 1. Leaf Carbon Economics And Energy Budgets**

Carbon is a universal currency of leaf economics. Ultimately, leaf energy budgets govern the rates of carbon assimilation that fuel plant growth and reproduction. Carbon economics thus constrains plant demography and influences plant fitness [84,85].

Across environments, natural selection has shaped plant form and function so that leaves must have a net positive return on resource investment [86]. The total mass of carbon assimilated by a leaf over its lifetime must be greater than the total mass of carbon invested in the leaf [87,88]. This can be expressed in terms of several key leaf functional traits as [84,89]

$$G = \frac{A_n L_f}{LMA} \cdot \frac{k_1}{k_2} = A_m L_f \cdot \frac{k_1}{k_2} \geq 1 \quad [I]$$

where  $G$  is lifetime carbon gain per unit carbon invested ( $\text{kg C kg C}^{-1}$ ),  $A_n$  is the peak net carbon assimilation rate per unit leaf area ( $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ),  $L_f$  is the functional leaf longevity (s),  $LMA$  is the leaf mass-to-area ratio ( $\text{kg m}^{-2}$ ),  $A_m$  is the peak net carbon assimilation rate per unit leaf mass ( $\mu\text{mol C g}^{-1} \text{s}^{-1}$ ),  $k_1$  is the molar mass conversion factor ( $\text{kg C } \mu\text{mol C}^{-1}$ ), and  $k_2$  is the carbon mass fraction ( $\text{kg C kg}^{-1}$ ). As we show, all these traits can ultimately be linked with leaf energy budgets. Further, differences in climate select for unique combinations of  $LMA$ ,  $A_n$ ,  $A_m$ ,  $L_f$  to promote thermal and metabolic stability of leaves.

Equation I shows that selection to maximize the return on carbon investment can be achieved in three ways: (i) selection to increase assimilation rate, (ii) selection to maximize leaf longevity, or (iii) selection to minimize  $LMA$  [84]. As we show, maximizing assimilation rates while simultaneously minimizing  $LMA$  must result from selection on leaf traits that govern the thermal and metabolic stability of leaves.

Collectively, these results demonstrate a potentially important limited homeothermy of plants, whereby plants experience variation in temperature that is small relative to air. This underscores the need for studies in physiology, ecology, and climate science to use plant (not only air) temperatures. New methodologies such as MODIS (moderate resolution imaging spectroradiometer) land surface temperature (e.g., [55–57]) and cellulose  $\delta^{18}\text{O}$  [11,47,58] offer considerable potential for estimating plant temperatures at macroecologically-relevant space and timescales.

**Why Photosynthesis-Weighted Leaf Homeothermy?**

We suggest that the mechanisms driving leaf homeothermy ultimately originate from natural selection on leaf carbon economics (Box 1). Specifically, selection to maximize lifetime net carbon gain across climate gradients has yielded (i) co-variation of climate and functional traits to maintain leaf temperatures near photosynthetic optima, and (ii) co-variation of thermal traits and leaf biochemistry to maximize net photosynthesis rates irrespective of environmental variation. For example, homeothermic leaf temperatures generally fall below 35–40°C (Figure 2), reflecting selection against the inactivation of Rubisco and photosynthesis at these temperatures [59]. As discussed below, an approximately similar leaf lifetime net carbon gain across climate gradients implies leaf homeothermy in both space and time. In the next section we review how energy budgets formalize the energetic processes linking climate and functional traits to plant temperature and metabolism.

**Energy Budgets Mechanistically Link Co-Variation in Traits and Climate to Plant Functioning**

Energy budgets combine the constituent energy fluxes (net radiation, convection, and evapotranspiration) that govern plant temperatures in response to environmental conditions (Box 2). The magnitudes and directions of the heat fluxes result from interactions of leaf functional traits (area, mass, width, dry matter content, absorptivity, inclination, orientation, and stomatal conductance) and environmental variables (net radiation, vapor pressure deficit, relative humidity, and air temperature). Energy budgets derive from thermodynamics and transport phenomena (cf. [60]). They play a foundational role in physiology and geoscience [3,10,52,54,61–66], and thus have a clear and direct relevance for trait-based ecology.

Energy budgets have been used to understand and predict plant temperatures and transpiration rates (e.g., [67,68,94–99]). They provide a theoretical basis for photosynthesis and eddy flux

## Box 2. Linking Energy Budgets And Leaf Functional Traits

Energy budgets equate heat fluxes at leaf surfaces with heat flux to storage in leaf mass (cf. [3,10,52,60,62,63,65]), such that:

$$R - C - \lambda E = S \quad [I]$$

where  $R$  ( $\text{W m}^{-2}$ ) is the net radiation flux,  $C$  ( $\text{W m}^{-2}$ ) is the convective (sensible heat) flux, and  $S$  ( $\text{W m}^{-2}$ ) is the storage flux. The evaporative (latent heat) flux  $\lambda E$  ( $\text{W m}^{-2}$ ) is the product of the latent heat of vaporization of water  $\lambda$  ( $\text{J kg}^{-1}$ ) and the transpiration rate  $E$  ( $\text{kg m}^{-2} \text{s}^{-1}$ ). As discussed below, Equation I shows how variation in key leaf functional traits can influence leaf energy balance. Equation I also provides a strong constraint on trait co-variation if natural selection has shaped leaf carbon economics. Additional derivations and definitions needed to elaborate this and the following equations are included in the Online Supplementary Material S1.

The net radiation flux of any object equals the difference between the radiation absorbed ( $R_{\text{abs}}$ ;  $\text{W m}^{-2}$ ) and emitted ( $R_{\text{emit}}$ ;  $\text{W m}^{-2}$ ), such that  $R = R_{\text{abs}} - R_{\text{emit}} = \alpha[R_{\text{sun}} + R_{\text{sky}} + R_{\text{ground}}] - \varphi^{-1}\epsilon\sigma T_l^4$ , where  $\alpha$  is the leaf absorptivity (dimensionless),  $R_{\text{sun}}$  ( $\text{W m}^{-2}$ ) is the shortwave radiation flux from the sun,  $R_{\text{sky}}$  ( $\text{W m}^{-2}$ ) is the longwave radiation flux from the sky,  $R_{\text{ground}}$  ( $\text{W m}^{-2}$ ) is the longwave radiation flux from the ground,  $\epsilon$  (dimensionless) is the leaf emissivity,  $\sigma$  ( $\text{W m}^{-2} \text{K}^{-1}$ ) is the Stefan–Boltzmann constant, and  $T_l$  (K) is the leaf temperature. The ratio of projected-to-total leaf area  $\varphi$  (dimensionless; 1/2 for flat leaves and  $1/\pi$  cylindrical leaves) accounts for emission of radiation from all sides of the leaf.

The convective flux is given by  $C = \rho_a c_{p,a} g_h [T_l - T_a]$ , where  $\rho_a$  ( $\text{kg m}^{-3}$ ) is the density of air,  $c_{p,a}$  ( $\text{J kg}^{-1} \text{K}^{-1}$ ) is the specific heat capacity of air, and  $T_a$  (K) is the air temperature. The boundary layer conductance to heat  $g_{b,h}$  ( $\text{m s}^{-1}$ ) is equivalent to the boundary layer conductance  $g_b$  ( $\text{m s}^{-1}$ ) and varies with leaf size and geometry.

When leaf temperature is constant in time, steady state conditions prevail and Equation I is reduced to the surface balance  $R - C - \lambda E = 0$ . After substitution and rearrangement using relationships from above and the Online Supplementary Material S1, the leaf temperature is given as

$$T_l = T_a + \frac{R\gamma[g_h/g_w]}{\rho_a c_{p,a} g_h [s + \gamma(g_h/g_w)]} - \frac{D}{s + \gamma(g_h/g_w)} \quad [II]$$

where  $\gamma$  ( $\text{Pa K}^{-1}$ ) is the psychrometric constant,  $g_w$  ( $\text{m s}^{-1}$ ) is the water vapor conductance,  $s$  ( $\text{Pa K}^{-1}$ ) is the slope of the saturation vapor pressure curve, and  $D$  (Pa) is the vapor pressure deficit. Note that leaf temperature is governed by several leaf functional traits, including leaf absorptivity (Equation S2 in the supplementary material online), leaf size and geometry (Equations S4 and S5), and stomatal conductance (Equation S7). The second term on the right in Equation II describes an increase of leaf temperature above air temperature that is proportional to net radiation. The third term describes a decrease of leaf temperature that is proportional to the vapor pressure deficit. Depending on the relative magnitudes of these terms, leaf temperature will be warmer than, cooler than, or equivalent to air temperature.

A Critical Integrative Functional Trait – The Thermal Time Constant  $\tau$ 

When leaf temperature varies in time, transient conditions prevail and relationships from above and the Online Supplementary Material S1 can be substituted into Equation I to give  $dT_l/dt = [T_e - T_l]/\tau$ . Here,  $T_e$  (K) is an equilibrium leaf temperature that is approached asymptotically through time, and  $\tau$  (s) is a thermal time constant. This thermal time constant is a key composite functional trait given by [52]

$$\tau = \frac{m_l c_{p,l}}{A_l [\rho_a c_{p,a} (g_{b,h} + g_r + g_w s / \gamma)]} \quad [III]$$

where  $g_r$  ( $\text{m s}^{-1}$ ) a radiation ‘conductance’ [52,63]. Notably,  $\tau$  (s) comprises several important functional traits, including leaf mass  $m_l$  (kg), specific heat capacity  $c_{p,l}$  ( $\text{J kg}^{-1} \text{K}^{-1}$ ), total two-sided surface area  $A_l$  ( $\text{m}^2$ ), size and geometry (Equations S4,S5) and stomatal conductance (Equation S7). Importantly, all functional traits in Equation III are for fresh leaves (i.e., including water). These equations can be solved analytically or numerically for various initial and boundary conditions [60,90] to predict leaf temperature in a variable environment (see Online Supplementary Material S1). The influence of leaf functional traits on the thermal time constant  $\tau$  is further examined in Box 3.

sensor technology [66] as well as models that predict weather and climate change effects on plant and ecosystem physiology [69–71]. Energy budgets are also important for understanding other ecological and physiological processes driven by plant temperature, such as plant–animal and plant–plant interactions [5,46,72,73].

Although the role of energy budgets as a driver of leaf trait–climate relationships has been recognized [13,42,43,74,75], only seldom have energy budgets been used for functional trait analyses (e.g., [7,8]). Indeed, the energetic links between climate, leaf functional traits, and leaf metabolism have not yet been fully articulated. However, this is becoming more feasible given



recent advances in microclimate modeling [76] and our growing understanding of plant biophysics [3,52,62,66] and metabolic ecology [20,77–79].

### The Energetic Basis of Leaf Homeothermy

The leaf energy budget of Equation II in Box 2 suggests that limited homeothermy (Figure 2A–D) originates from variation in climate variables and/or leaf traits across air temperature gradients. If leaf traits are invariant with air temperature, Equation II in Box 2 suggests that two meteorological processes drive the observed limited homeothermy: (i) a general decrease in the slope of the saturation vapor pressure curve  $s$  with air temperature, leading to an increase in leaf temperature excess ( $T_l - T_a$ ) at low air temperatures, and (ii) a general increase in vapor pressure deficit with air temperature, leading to a decrease in leaf temperature excess at high air temperatures [10,63]. Indeed, even a wet wash rag with an infinite surface conductance will exhibit limited homeothermy [10]. However, because leaf traits are not constant but instead co-vary with climate [26–29], Equation II in Box 2 implicates both climate and leaf traits as co-drivers of limited leaf homeothermy.

### Linking Functional Traits, Transient Temperatures, and Carbon Economics of Leaves

The thermal response time of a leaf to changes in surface energy fluxes is characterized by the thermal time constant  $\tau$  (s; Equation III in Box 2). The thermal time constant is a critical trait underlying leaf carbon economics. It is a composite leaf trait that comprises several additional traits, including dry matter mass, water mass, specific heat capacity, total (two-sided) surface area, width, geometry (e.g., broadleaf or needle-leaf), and stomatal conductance. These traits are combined into a single ratio  $\tau$  that quantifies the ability of the leaf to store heat versus its ability to exchange heat with the environment (Box 2). Inspection of Equation S16 in the supplementary material online shows that the thermal time constant equals the time required for leaf temperature  $T_l$  to reach  $e^{-1} \approx 37\%$  of the way through the temperature difference  $T_{e,2} - T_{e,1}$ . Thus, smaller time constants correspond to leaves that respond more rapidly to changes in surface energy fluxes (e.g., from sunflecks, wind gusts and lulls, etc.), while longer time constants correspond to leaves that respond more slowly to changes in surface fluxes. For leaves,  $\tau$  generally varies from a few seconds to several minutes [3,52], but can be up to several hours [80].

#### Box 3. Influences of Leaf Functional Traits on a Key Integrative Trait – The Thermal Time Constant

The thermal time constant  $\tau$  (s; Equation III in Box 2) is influenced by several key functional traits: leaf mass, specific heat capacity, total surface area, size, geometry, stomatal conductance, leaf mass per area, and leaf dry matter content (i.e., water content). Leaf mass per area (LMA;  $\text{kg m}^{-2}$ ) is the ratio of dry leaf mass  $m_{l,d}$  (kg) to projected leaf area  $\varphi A_l$  ( $\text{m}^2$ ), or  $LMA = m_{l,d}/\varphi A_l$ , where  $\varphi$  (dimensionless; taken as 1/2 for flat leaves and  $1/\pi$  for cylindrical leaves) is the ratio of projected-to-total leaf area, and  $A_l$  ( $\text{m}^2$ ) is the total surface area of a fresh leaf [91]. Leaf dry matter content (LDMC;  $\text{kg kg}^{-1}$ ) is the mass fraction of dry matter in a fresh leaf, or  $LDMC = m_{l,d}/m_l$ , where  $m_l$  (kg) is the fresh leaf mass including water. LDMC is a key allocation trait relative to leaf carbon economics [92,93].

Recognizing that  $m_l/A_l = \varphi LMA/LDMC$ , Equation III in Box 2 can be rewritten to explicitly show that many traits underlie  $\tau$ , because  $\tau = [\varphi LMA/LDMC] \cdot [c_{p,l}/h]$  where  $c_{p,l}$  ( $\text{J kg}^{-1} \text{K}^{-1}$ ) is the specific heat capacity of the fresh leaf including water, and  $h$  ( $\text{W m}^{-2} \text{K}^{-1}$ ) is an overall heat transfer coefficient (see Online Supplementary Material S1). Importantly, the thermal mass in the above equation comprises masses of both leaf dry matter and leaf water.

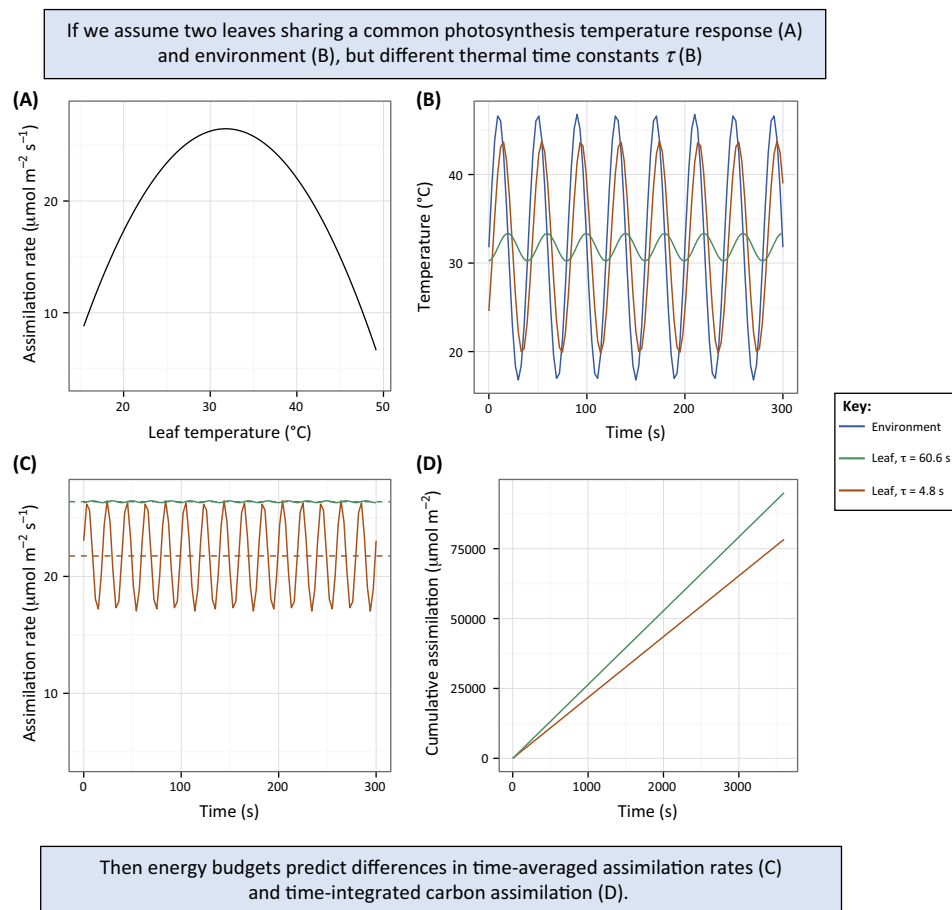
Next, we can include the dependence of the specific heat capacity  $c_{p,l}$  on leaf water content. From the simple rule of mixtures, we have  $c = LDMC \cdot c_{p,d} + (1 - LDMC) \cdot c_{p,w}$ , where  $c_{p,d}$  ( $\text{J kg}^{-1} \text{K}^{-1}$ ) and  $c_{p,w}$  ( $\text{J kg}^{-1} \text{K}^{-1}$ ) are the specific heat capacities of dry leaf matter and water, respectively. Substitution into the above relation between  $\tau$ , LMA, and LDMC gives:

$$\tau = \varphi LMA \left( \frac{c_{p,w}}{LDMC \cdot h} + \frac{c_{p,d} - c_{p,w}}{h} \right) \quad [I]$$

This relationship reveals the influence of LMA and LDMC on thermal time constants, and also accounts for the influence of leaf water content on leaf thermal mass [7] and leaf specific heat capacity.

The thermal time constant  $\tau$  can be written in terms of two often-measured functional traits (Box 3): leaf mass per area (LMA;  $\text{kg m}^{-2}$ ) and leaf dry matter content (LDMC; dimensionless). LMA is a key trait in the leaf economics spectrum given its relevance for carbon cost, mechanical resistance, and lifespan of leaves [81,82]. However, LMA also has strong implications for the thermal response of a leaf (Box 3). It influences leaf temperature dynamics and can help to maintain leaves near photosynthetic optima [83]. Consistent with this are recent results showing that leaf thickness promotes lethal temperature avoidance [6–8]. Further, given the role of LMA in thermal time constants, and correlation of LMA with other thermal traits [42], it is likely that the global leaf economics spectrum [82] reflects not only carbon economics (Box 1) but also the thermal traits and energy budgets that govern them.

The links between the thermal time constant, leaf temperature dynamics, instantaneous photosynthetic rates, and time-integrated carbon assimilation are illustrated in Figure 3. Here we



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**Figure 3. Effects of Variation in the Thermal Time Constant  $\tau$  on Simulated Leaf Temperatures, Net  $\text{CO}_2$  Assimilation Rates, and Cumulative Time-Integrated Net  $\text{CO}_2$  Assimilation.** This illustration considers two leaves that have different time constants ( $\tau = 4.8$  s and  $\tau = 60.6$  s; data from [52]) but share a common photosynthesis temperature response (A; data from [53]) and environment (B). Differences in the time constant  $\tau$  lead to differences in leaf temperature dynamics (B), instantaneous assimilation rates (C), and cumulative assimilation over time (D). If natural selection has optimized co-variation of energy budgets and photosynthetic biochemistry to maximize short-term carbon assimilation in leaf carbon economics, we would expect a strong relationship between thermal time constants and the leaf temperature ranges for optimal photosynthesis (i.e., the breadths of photosynthesis temperature response curves). Leaf temperatures were calculated using (Equation S21) with environmental forcing ( $\Delta T_e = 15^\circ\text{C}$  and  $f = 0.025$  Hz; data from [8]) that is consistent with empirical measurements [3,52]. Broken lines indicate time-averaged assimilation rates.



consider two leaves with different thermal time constants [52], but a common photosynthesis temperature response (Figure 3A) [53] and a common environment (Figure 3B; Equation S17). A difference in the thermal time constant alone can lead to large differences in leaf temperatures (Figure 3B), instantaneous assimilation rates (Figure 3C), and ultimately time-integrated carbon assimilation (Figure 3D). All else equal, the leaf with the smaller time constant will have a more variable leaf temperature and instantaneous assimilation rate; consequently, this leaf will have a lower time-averaged assimilation rate and yield a smaller total time-integrated carbon assimilation. Thus, if natural selection on both the thermal time constant and photosynthesis temperature response has optimized instantaneous assimilation rates to maximize total 'lifetime' time-integrated assimilation, our theory predicts an inverse relationship between the time constant  $\tau$  (thermal stability) and the breadth of the photosynthesis temperature response curve  $T_{90}$  (photosynthetic stability; see Online Supplementary Material S1).

The predicted inverse relationship between  $\tau$  and  $T_{90}$  reflects a deeper trade-off between leaf metabolic and thermal stability. This tradeoff has two important implications for leaf carbon economics. First, it means that thermally unstable leaves are photosynthetically stable (and vice versa), which promotes an overall metabolic homeostasis that helps to maintain rates of time-averaged assimilation near peak values. Thus, selection to maximize assimilation should be seen as not only operating on peak assimilation rates but also on  $\tau$  and  $T_{90}$ . Second, it provides a mechanism by which selection can simultaneously maximize peak  $\text{CO}_2$  assimilation rates while minimizing LMA (Box 1). This would otherwise be impossible given the contrasting effects of LMA on leaf carbon cost and thermal stability; for example, leaves with low LMA have a low carbon cost but are thermally unstable, and without the inverse relationship between  $T_{90}$  and  $\tau$  would also be photosynthetically unstable. Thus, this inverse relationship provides a mechanism that enables plants to minimize LMA while maintaining photosynthetic stability and maximizing both time-averaged and time-integrated carbon assimilation. Future studies should empirically test this prediction given its profound potential for linking climate, functional traits, energy budgets, homeothermy, and leaf carbon economics.

### Concluding Remarks

Our analyses of both point and photosynthesis-weighted leaf temperature data support a limited homeothermy of leaves across temperature and climate gradients. This suggests that directional selection and environmental filtering on multiple plant traits has led to an approximate convergence of plant metabolism across climate gradients. These observations are supported by a theory of leaf economics, as well as by empirical data of plant growth and production across broad temperature gradients. Through a general theory of carbon economics derived from energy budgets, the observed shift in leaf traits across broad temperature gradients appears to result in the maintenance of leaf temperatures near photosynthetic optima and below the inactivation temperature of Rubisco. This viewpoint indicates that natural selection has honed leaf biophysics to maximize carbon assimilation in the face of variable environmental temperatures. An important implication is that air temperature is a poor proxy for leaf temperature, particularly during periods of peak photosynthesis. Consequently, these results reiterate a need for studies in plant, ecosystem, and global change ecology to measure the metabolically-relevant plant tissue temperatures and not air temperatures as has traditionally been done.

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## Supplementary Information

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