

Commentary

Cold-blooded forests in a warming world

Introduction

Leaf temperature influences almost all physiological processes in leaves, and consequently, is one of the most important drivers of carbon, water, and energy fluxes through ecosystems. Plants have many ways of regulating temperature, both actively and passively, to maximize carbon uptake and minimize water loss. Photosynthesis is particularly sensitive to temperature, as it increases with warming to a threshold, and then declines (Berry & Björkman, 1980). Because measuring leaf temperatures can be challenging, many vegetation process models use air temperature to drive plant physiological function (Blum, *et al.*, 2013). Recent studies have argued, however, that air temperature (T_{air}) is not an appropriate proxy for leaf temperature (T_{leaf}) (Michaletz *et al.*, 2016; Dong *et al.*, 2017; Fauset, *et al.*, 2018). At the same time, recent analyses of oxygen isotopes (^{18}O) in wood cellulose have revealed that photosynthesis is most often occurring at temperatures of *c.* 21°C, suggesting a remarkably consistent signal of leaf thermoregulation across the globe (Helliker & Richter, 2008; Song *et al.*, 2011). In this issue of *New Phytologist*, Drake *et al.* (2020; pp. 1511–1523) link these two distinct fields of study for the first time: the biophysical and the isotopic aspects of leaf thermodynamics. This study provides two important contributions: (1) a case study showing a surprising lack of leaf thermoregulation in whole tree crowns; and (2) the first direct, independent validation of the tree ring ^{18}O method for reconstructing past leaf temperatures at the whole-tree level. Drake *et al.* leveraged a unique whole-tree chamber experiment to investigate carbon flux and canopy thermodynamics. Twelve chambers enclosing individual *Eucalyptus parramattensis* trees were instrumented for continuous measurements of T_{air} , T_{leaf} , and tree-level carbon dioxide (CO_2) uptake for nine months. A +3°C warming treatment, a shorter-term heat wave treatment, and seasonal variation allowed for a wide range of air temperatures to investigate (−1 to 45°C). The whole-tree chambers provided the high level of control that glasshouse and growth chamber studies have, while also allowing for continuous

carbon and water flux data for full-size trees grown *in situ*, a scenario that is notoriously difficult to achieve.

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A surprising lack of leaf thermoregulation

Leaves can be hotter than air due to solar radiation, or cooler than air by increasing evapotranspiration through stomata. These effects are, in turn, influenced by canopy structure, leaf morphology, stomatal density and size, soil moisture, wind, and relative humidity. As such, the predictability of T_{leaf} is rather complex and has been the subject of study for decades. Historically, terminology was borrowed from animal thermoregulation, where ‘poikilothermy’ occurs when body temperatures equal ambient temperatures (i.e. cold-blooded); and ‘homeothermy’ occurs when body temperatures remain within narrow tolerance ranges (i.e. warm-blooded) (Gates, 1965). True homeothermy (sometimes called ‘homeostasis’, when T_{leaf} is constant), is rare in plants. Thus, we have ‘limited homeothermy’ (Mahan & Upchurch, 1988), where leaves are slightly cooler than air at high temperatures and slightly warmer than air at low temperatures. This has also been called ‘biophysical homeostasis’ (Dong *et al.*, 2017), but I argue that this particular terminology is too easily confused with the ‘constant T_{leaf} scenario’, and best avoided. The most useful way to define thermal responses of plants is to consider the slope of the relationship between T_{leaf} and T_{air} (Fig. 1) (Blonder & Michaletz, 2018). Here, poikilothermy occurs when the slope = 1, homeostasis (or true homeothermy) occurs when the slope = 0, and limited homeothermy occurs when the slope is between 0 and 1. ‘Megathermy’ occurs when the slope is greater than 1, often in desert plants or forest canopy sun leaves (Doughty & Goulden, 2008; Dong *et al.*, 2017; Rey-Sanchez *et al.*, 2017; Fauset *et al.*, 2018).

Drake *et al.* found T_{leaf} of upper tree crowns nearly equaled T_{air} under all but the most extreme climatic conditions, and concluded that these trees were nearly poikilothermic. They found no evidence of ‘limited homeothermy’, and a surprising lack of thermoregulation altogether. Leaves were more than 3°C greater than T_{air} only with high radiation but low stomatal conductance, which was rare in this dataset. Leaves also were sometimes cooler than air, but only at night. In the context of modeling, this strong control of T_{air} on T_{leaf} implies that T_{air} can be a reasonable proxy for T_{leaf} at least in some systems.

This article is a Commentary on Drake *et al.* (2020), **228**: 1511–1523

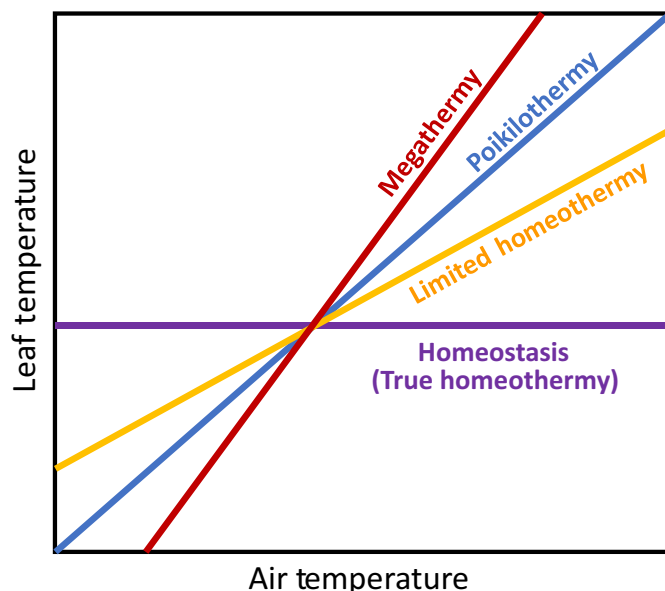


Fig. 1 Simplified illustration of how the slope of the leaf : air temperature relationship can help to define plant thermoregulation strategies. Poikilothermy occurs when the slope = 1, limited homeothermy occurs when the slope is between 0 and 1, homeostasis (or true homeothermy) occurs when the slope = 0, and megathermy occurs when the slope is greater than 1.

First tree-level confirmation of ^{18}O isotope method for reconstructing leaf temperatures

Recent studies have explored using stable oxygen isotopes of wood to reconstruct canopy temperatures at which plants were most often photosynthesizing (Helliker & Richter, 2008). The amount of ^{18}O found in the cellulose of wood corresponding to a specific time of growth (e.g. a tree ring) can be used to calculate the internal leaf vapor pressure for this time period, from which T_{leaf} can be derived. This estimation of T_{leaf} is weighted towards times when photosynthesis is highest, and therefore is called 'carbon assimilation-weighted leaf temperature' (T_{LAW}). As such, this method cannot estimate actual leaf temperature or identify when T_{leaf} is decoupled from T_{air} . Despite these constraints, this method has shown remarkable global convergence, with T_{LAW} values of $21.4 \pm 2.2^\circ\text{C}$ across 50° latitude, from boreal to subtropical ecosystems (Helliker & Richter, 2008; Song *et al.*, 2011). To date, this method has been validated at the ecosystem level (Helliker *et al.*, 2018), but never at the individual-tree level or for time periods less than one year. Due to the rapid growth rate of their study species (9 m tall in the first year), Drake *et al.* were able to isolate ^{18}O from wood for very narrow time periods (*c.* 1 month) to compare with concurrent measurements of canopy-level T_{leaf} and CO_2 uptake. This enabled the first direct validation of the cellulosic ^{18}O method for estimating the temperature of carbon assimilation for individual trees. Drake *et al.* also investigated patterns of thermoregulation of both T_{leaf} and T_{LAW} . They found that even when leaf temperature was weighted by high rates of photosynthesis, it was still strongly driven by T_{air} . While this study did not reveal a constant, homeostatic T_{LAW} , it ultimately represents only one site, and the mean values of T_{LAW} (20.9 and 23.5°C for control and warmed

chambers, respectively) fall neatly within the broad pattern of global convergence found by both Helliker & Richter (2008) and Song *et al.* (2011). This work represents an important validation of the cellulosic ^{18}O approach, which promises to be an inexpensive means of integrating temperatures of leaf function across space and time, from leaf to landscape and even across the centuries.

Future directions: species variation, canopy structure, and physiological acclimation

The whole-tree chambers provided unprecedented measurements, but also resulted in limitations ripe for future investigation. One of the trade-offs for high precision data is the logistical necessity to focus on one species. There may be a trait spectrum of thermoregulation capacity, however, where species with wide leaves and low stomatal conductance have limited capacity to keep leaves cooler than air, while narrow leaves with greater stomatal conductance may be better able to thermoregulate (Fauset *et al.*, 2018). Narrow leaves allow for greater evaporative cooling because of thinner leaf boundary layers and less resistance to vapor diffusion. Species with greater stomatal size or density could also have greater cooling capacity compared to conspecifics (Schymanski *et al.*, 2013). Thermoregulation strategies across a broader swath of species remains unexplored.


Another potential limitation of the study is that Drake *et al.* measured T_{leaf} of only upper-canopy sun leaves, yet measured CO_2 assimilation of the entire crown. It may be a reasonable assumption that whole-tree photosynthetic uptake is influenced most by sun leaf temperatures because upper canopies can represent a disproportionate amount of total forest carbon uptake (Doughty & Goulden, 2008). However, uppermost foliage can also act as a protective shield (i.e. 'umbrella effect'), absorbing much of the incoming radiation and allowing mid-canopy leaves to have a greater capacity for carbon assimilation than sun leaves (Ishii *et al.*, 2004). Indeed, the vertical variation in leaf thermoregulation within forest canopies has rarely been investigated, and could depend on seasonal water availability (Rey-Sanchez *et al.*, 2017). Since the trees in Drake *et al.* were never water stressed and wind was uniformly low inside the chambers, the response of stomatal conductance (and its potential for evaporative cooling) may not be representative of *in situ* conditions.

The poikilothermy found in Drake *et al.* could be interpreted as a lack of thermoregulation capacity. If plants are not able to maintain temperatures below critical thresholds where damage occurs, then physiological acclimation becomes critical for plants to keep photosynthesizing. In other words, species that cannot thermoregulate will need to rely on biochemical mechanisms to deal with the heat of a rapidly warming world. This trade-off has been described as a spectrum, with maximum 'leaf thermal stability' at one extreme, and maximum 'thermal breadth of photosynthesis' (the ability to maintain maximum photosynthesis rates across wider temperature ranges) at the other extreme (Michaletz *et al.*, 2016). Finding more evidence of these linkages between thermoregulation capacity and photosynthetic acclimation capacity remains a cutting-edge challenge in this field.

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References

- Berry J, Björkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **31**: 491–543.
- Blonder B, Michaletz ST. 2018. A model for leaf temperature decoupling from air temperature. *Agricultural and Forest Meteorology* **262**: 354–360.
- Blum M, Lensky IM, Nestel D. 2013. Estimation of olive grove canopy temperature from MODIS thermal imagery is more accurate than interpolation from meteorological stations. *Agricultural and Forest Meteorology* **176**: 90–93.
- Dong N, Prentice IC, Harrison SP, Song QH, Zhang YP. 2017. Biophysical homeostasis of leaf temperature: a neglected process for vegetation and land-surface modelling. *Global Ecology and Biogeography* **26**: 998–1007.
- Doughty CE, Goulden ML. 2008. Are tropical forests near a high temperature threshold? *Journal of Geophysical Research–Biogeosciences* **113**: G00B07.
- Drake JE, Harwood R, Vårhammar A, Barbour MM, Reich PB, Barton CVM, Tjoelker MG. 2020. No evidence of homeostatic regulation of leaf temperature in *Eucalyptus parramattensis* trees: integration of CO₂ flux and oxygen isotope methodologies. *New Phytologist* **228**: 1511–1523.
- Fauset S, Freitas HC, Galbraith DR, Sullivan MJP, Aidar MPM, Joly CA, Phillips OL, Vieira SA, Gloor MU. 2018. Differences in leaf thermoregulation and water use strategies between three co-occurring Atlantic forest tree species. *Plant, Cell & Environment* **41**: 1618–1631.
- Gates D. 1965. Energy, plants, and ecology. *Ecology* **46**: 1–13.
- Helliker BR, Richter SL. 2008. Subtropical to boreal convergence of tree-leaf temperatures. *Nature* **454**: 511–U516.
- Helliker BR, Song X, Goulden ML, Clark K, Bolstad P, Munger JW, Chen JQ, Noormets A, Hollinger D, Wofsy S *et al.* 2018. Assessing the interplay between canopy energy balance and photosynthesis with cellulose $\delta^{18}\text{O}$: large-scale patterns and independent ground-truthing. *Oecologia* **187**: 995–1007.
- Ishii HT, Tanabe S, Hiura T. 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science* **50**: 342–355.
- Mahan JR, Upchurch DR. 1988. Maintenance of constant leaf temperature by plants. 1. Hypothesis limited homeothermy. *Environmental and Experimental Botany* **28**: 351–357.
- Michaletz ST, Weiser MD, McDowell NG, Zhou JZ, Kaspari M, Helliker BR, Enquist BJ. 2016. The energetic and carbon economic origins of leaf thermoregulation. *Nature Plants* **2**: 16129.
- Rey-Sanchez AC, Slot M, Posada JM, Kitajima K. 2017. Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest. *Climate Research* **71**: 75–89.
- Schymanski SJ, Or D, Zwieniecki M. 2013. Stomatal control and leaf thermal and hydraulic capacitances under rapid environmental fluctuations. *PLoS ONE* **8**: e54231.
- Song X, Barbour MM, Saurer M, Helliker BR. 2011. Examining the large-scale convergence of photosynthesis-weighted tree leaf temperatures through stable oxygen isotope analysis of multiple data sets. *New Phytologist* **192**: 912–924.

Key words: canopy temperature, carbon assimilation-weighted leaf temperature, cellulosic ^{18}O , homeostasis, homeothermy, poikilothermy, thermoregulation.