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When a cuvette is not a canopy: A caution about measuring leaf temperature during gas exchange measurements

Christopher J. Still[a,*], Adam Sibley[a], Gerald Page[a], Frederick C. Meinzer[a,b], Sanna Sevanto[c]

[a] Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA
[b] USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, USA
[c] Earth and Environmental Science Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA

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ABSTRACT

Plant gas exchange systems are widely used to study leaf physiological processes and properties such as stomatal function and the maximum carboxylation rate of Rubisco. Increasingly, these systems are used to assess how leaf gas exchange varies with temperature in order to better understand how rising temperature will impact plant function. Examples of such studies include variation in optimal temperatures of photosynthesis as a function of species and growth environment, and respiratory acclimation to higher temperatures. Leaf thermoregulation leading to homeothermy has been reported based on leaf gas exchange measurements spanning a large (~25 °C) temperature range. However, as we show here, the design of a popular gas exchange system used for temperature-response measurements can lead to biased measurements of leaf temperature. We demonstrate this with an example showing that apparent leaf thermoregulatory behavior can arise even in empty cuvettes. More broadly, our results have implications for other temperature manipulations in similar gas exchange systems.

1. Introduction

Leaf temperature is an important parameter used in calculating plant gas exchange with the environment. It determines the concentration of water vapor at saturation vapor pressure inside the stomata and influences the concentration gradient driving gas exchange with the environment as well as rates of photosynthesis and respiration (Monteith and Unsworth, 2013; Jones, 2013; Yamori et al., 2014; Slot et al., 2016). Therefore, leaf temperature is critical in analysis of gas exchange measurements (e.g., Long et al., 1996), and for calculating plant gas exchange in vegetation models at scales ranging from leaves to ecosystems (Dewar, 2002; Bonan et al., 2014). Experiments designed to study the response of leaf gas exchange to varying temperature are increasingly common (e.g., Yamori et al., 2014; Atkin et al., 2015) and are important for improved model predictions of climate change impacts on vegetation carbon cycling, mortality, and species composition.

Variations in leaf temperature, and possible consequences to plant function as well as to interpretation of gas exchange measurements, is an active field of research (Leigh et al., 2012; Leigh et al., 2017; Cernusak et al., 2018). Because of the centrality of leaf temperature in so many critical plant processes, its variation with air temperature has been studied for decades (Linacre, 1964, 1967; Gates, 2012). Theoretically, small leaves remain closer to ambient temperature than large leaves (Leigh et al., 2012), and deviations below ambient are mostly due to evaporative cooling when stomata are open and boundary layer conductance to heat and vapor transfer is high (Leigh et al., 2017; Blonder and Michaletz, 2018). Conversely, above-ambient temperatures are commonly observed in situations of high net radiation when stomatal and boundary layer conductances are low (Leigh et al., 2017).

Several recent analyses argue that leaves regulate their temperatures to remain cooler than air beyond a crossover temperature, and thus mitigate the impacts of high temperature on plant function (Michaletz et al., 2015, 2016; Dong et al., 2017; Blonder and Michaletz, 2018). This thermoregulatory behavior has been described as “leaf homeothermy” (or homeostasis – Dong et al., 2017). Specifically, homeothermy describes the phenomenon whereby at lower air temperature (T_{air}), leaf temperature (T_{leaf}) is warmer than ambient, while T_{leaf} is cooler than T_{air}. above an ‘equality air temperature.’ Operationally, the existence of leaf homeothermy has been defined as occurring when the slope of T_{leaf} plotted against T_{air} is less than 1 (Michaletz et al., 2015, 2016; Blonder and Michaletz, 2018). Many of the initial datasets that supported the leaf homeothermy hypothesis were collected in controlled environments using crop plants selected for very high transpiration rates (Linacre, 1964, 1967). While these data have been reanalyzed and used to support the occurrence of leaf homeothermy (Michaletz et al., 2015, 2016), it remains unclear to what

* Corresponding author.
E-mail address: chris.still@oregonstate.edu (C.J. Still).

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extent leaf homeothermy commonly occurs in natural ecosystems (Fauset et al., 2018).

Recently, T_{leaf} and T_{air} data from a large number of sites in the south-west USA was published (Blonder and Michaletz, 2018). Curiously, leaves measured under ambient conditions did not exhibit homeothermy, whereas measurements made by manipulating T_{air} using a gas-exchange chamber did. While these data were presented as evidence to support the existence of homeothermy in natural ecosystems, it led us to question whether the purported leaf homeothermy could be a result of an experimental artifact induced by the gas-exchange system itself. In this study, we present and analyze experimental results from gas exchange measurements made on needleleaf species and using empty chambers without leaves subjected to similarly large T_{air} variations. We contrast our measurements with those presented in the literature and discuss more broadly how T_{leaf} measurements made with these widely used gas exchange systems can be subject to misinterpretation.

2. Materials and methods

As part of a larger campaign, we designed an experiment to test for the presence of measurement biases in $T_{leaf} - T_{air}$ introduced by using LI-COR LI-6400-XT gas exchange instruments with Expanded Temperature Control Kits (similar to systems used by Blonder and Michaletz, 2018). We recorded temperature response curves on two conifer species (one-seed juniper, *Juniperus monosperma,* and pinyon pine, *Pinus edulis*), as well as an empty cuvette, using two LI-6400XT systems. For these measurements, photosynthetically active radiation (PAR) was set to 2000 μmol m^{-2} s^{-1}. A low flow rate of 200 μmol s^{-1} was used to reduce the influence of ambient air on cuvette temperature and to maximize the signal-to-noise ratio of the gas concentration measurements used to estimate fluxes. Total boundary layer conductance varied with leaf area in the chamber, and for the experiments reported here was 2.56 mol m^{-2} s^{-1} (juniper) and 1.11 mol m^{-2} s^{-1} (pine). A constant reference relative humidity of 15% and a CO_2 reference concentration of 400 ppm broadly representative of the ambient conditions at our experimental site were maintained during all measurements. The 15% relative humidity is also the highest attainable humidity at the high end of our air temperature range (50 °C) without adding water vapor to the airstream. For this study, a subset of measurements on juniper and pinyon pine trees grown in ambient conditions in Los Alamos, New Mexico was selected for analysis. The samples were collected from the Los Alamos Survival-Mortality (SUMO) experiment (e.g., Grossiord et al., 2017) located in Los Alamos County, New Mexico (35.49°N, 106.18°W, 2175 m a.s.l) in Aug 2018. Branches ~30 cm long were cut from the control trees (growing naturally without manipulation) of the SUMO experiment and placed in a bucket with the cut ends in full contact with water. The branches were transported to the laboratory for measurements and stored with full access to water in a growth chamber set to mimic outside conditions. Just prior to being measured in the LI-6400 the cut end of each branch was placed in a plastic vial filled with water to maintain unlimited water access. For each branch sample we selected an appropriately sized section of foliage to fill the LI-6400 cuvette and enclosed it. Care was taken to ensure foliage was in direct contact with the leaf temperature thermocouple inside the cuvette, though it should be noted that contact is difficult to guarantee with needleleaf species. After measurements were completed, the shoot section that was in the cuvette was excised and projected leaf area was measured by scanning the green needles from the shoot and measuring their cumulative area using the "analyze particle" function in ImageJ.

In order to vary the temperatures leaves were exposed to during measurements, each gas exchange instrument was fitted with a 6400-88 Expanded Temperature Control Kit. In the LI-6400XT system an aluminum block surrounds the cuvette chamber on the sensor head. The temperature of this block (T_{block}) is controlled within 5 °C of ambient temperature by two built in Peltier heaters and two cooling fans. The 6400-88 Expanded Temperature Control Kit consists of two hollow metal blocks through which water can be run to expand the block temperature control to any value between >1 °C and 50 °C. When installed, this kit is sandwiched between the Peltier heater and cooling fan on either side of the block. We used a water reservoir, to which ice or boiling water could be added, and a pump to circulate water warmed/cooled to near our desired T_{block} through this unit. For this experiment we stepped through T_{block} values of 10, 15, 20, 25, 30, 40, and 50 °C with leaves from each species, and then with empty cuvettes (no leaves in the cuvettes). By setting target T_{block} to our desired temperature on the LI-6400XT at each step, the internal algorithms of the instrument made micro-adjustments via the fans and Peltier heaters to maintain stable T_{block} values for long periods of time.

The temperature of the block (T_{block}) is measured by a factory-installed thermistor. T_{air} on the LI-6400XT is measured by a factory-installed thermistor located just above the mixing fan on the bottom of the cuvette. Finally, the temperature of the abaxial surface of a leaf in the cuvette, T_{leaf_m}, is measured via direct contact with a fine-wire thermocouple inside the cuvette. As part of our experiment was run with an empty cuvette, this thermocouple was reading the air temperature at the usual measurement location of T_{leaf_m}. As we stepped through our desired block temperatures when the cuvettes were empty, we waited for T_{leaf_m} readings to stabilize using a very conservative definition of stability – in some cases waiting up to 40 min - before a measurement was recorded. Thermocouples for measuring leaf temperatures (i.e., T_{leaf_m}) were then replaced by new ones in both machines, and the empty cuvette measurements repeated to ensure they were free from errors introduced by faulty fine-wire thermocouples. In what follows, for measurements with and without leaves in the cuvettes, temperature measured by the leaf thermocouples is referred to as T_{leaf_m}, while the temperature of air measured by the factory-installed thermistor inside the cuvette is called T_{air}. In addition to direct measurements, leaf temperature can also be calculated using energy balance equations programmed into the Licor Li-6400's operating system. We refer to this calculated leaf temperature as T_{leaf_eb}.

3. Results and discussion

Temperature measurements on both the juniper and pine leaves show evidence of the same limited homeothermy described by Blonder and Michaletz (2018), with a plot of T_{leaf_m} versus T_{air} for both species showing slopes below 1 (Fig. 1a). Similarly, as seen in Fig. 1b, T_{leaf_m} is higher than T_{air} below the equality temperature and lower than T_{air} above the equality temperature (~25 and 27 °C for pine and juniper, respectively, which are in the range of laboratory air temperature during the experiments). However, leaf temperature values based on energy balance theory, and calculated by software using data from the cuvette (i.e., T_{leaf_eb}), suggest a very different interpretation (Fig. 1c). For both species, the best fit line of T_{leaf_eb} versus T_{air} has a slope slightly larger than 1, with no evidence of a decreasing slope at higher T_{air} as would be required by homeothermy. The slope is slightly larger for pinyon pine, as would be expected based on its lower boundary layer conductance and transpiration compared to the juniper. In both species, transpiration (and thus evaporative cooling) peaks between 20 and 30 °C (Fig. 1d), and declines at higher temperatures following sharp decreases of stomatal conductance (g_s) in response to increasing vapor pressure deficit (VPD), which in our experiments exceeded 5 kPa at the highest temperatures. Such a response of g_s to VPD is to be expected (e.g., Schulze et al., 1972). Thus, leaf homeothermy cannot be occurring, as the principal process that could account for cooling of leaves at high temperatures (transpiration) declines with increasing temperature.

What could account for the apparent homeothermy implied in Figs. 1a and b? Our temperature data measured without leaves in the cuvette are also consistent with homeothermy (Fig. 2). An ordinary least squares linear regression with T_{leaf_m} on the y-axis and T_{air} on the

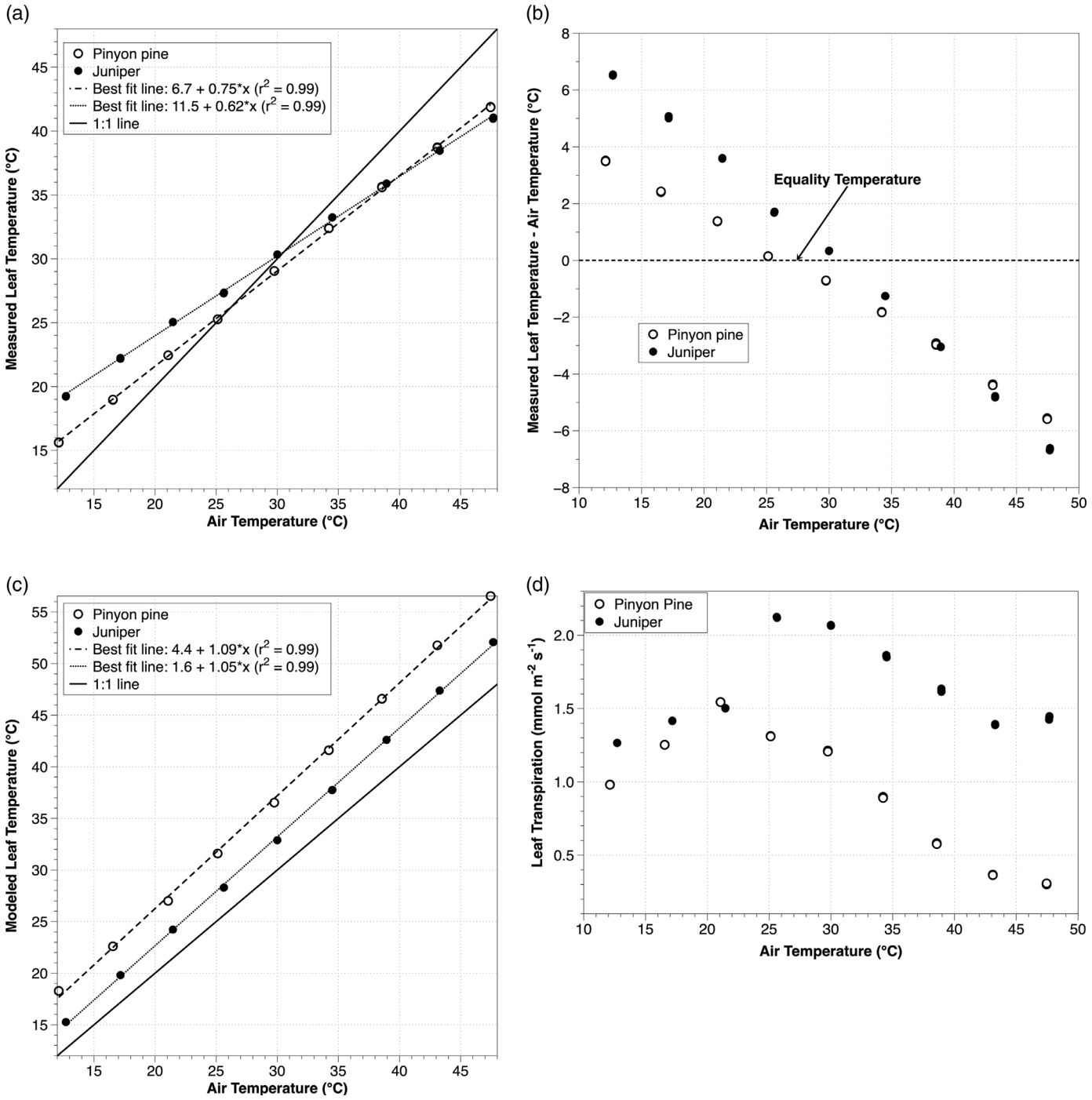

Fig. 1. (a) T_{leaf_m} versus T_{air} as measured in two different species (open and filled symbols represent pinyon pine and one-seed juniper, respectively). Dotted and dash-dot lines are linear regression model fits of species-specific data, solid line is 1:1. (b) $T_{leaf\_m} - T_{air}$ against T_{air} for two different species (open and filled symbols represent pinyon pine and one-seed juniper, respectively). Equality temperature occurs where $T_{leaf\_m} = T_{air}$. (c) Calculated T_{leaf_eb} versus T_{air} from the same experiments. Open and filled symbols represent pinyon pine and one-seed juniper, respectively. Dotted and dash-dot lines are linear regression model fits of species-specific data, solid line is 1:1. T_{leaf_eb} is based on energy balance theory and measured chamber conditions and transpiration fluxes. (d) Measured leaf transpiration versus T_{air} in two different species (open and filled symbols represent pinyon pine and one-seed juniper, respectively).

x-axis produced a slope of 0.64 (Fig. 2a), similar to the slopes for juniper and pinyon pine shown in Fig. 1a and also to previous reports of leaf homeothermy (Michaletz et al., 2015, 2016; Blonder and Michaletz, 2018). At temperatures below the so-called equivalent temperature (~27 °C), the fine-wire thermocouple inside the empty cuvette (normally in contact with a leaf to record its temperature) measured higher values than the thermistor that measures air beneath the cuvette (i.e., $T_{leaf\_m} - T_{air} > 0$). At air temperatures above the equality temperature, the opposite pattern occurs (i.e., $T_{leaf\_m} - T_{air} < 0$) as seen in Fig. 2b. In other words, the engineering design of the gas exchange system itself induces apparent homeothermy: $T_{leaf\_m} > T_{air} > T_{block}$ at T_{block} below ~27 °C and $T_{leaf\_m} < T_{air} < T_{block}$ at higher temperatures (27 °C was the ambient air temperature in the laboratory during these measurements).

These temperature patterns reflect the way temperature is controlled in the LI-6400 XT gas exchange cuvette, specifically, the

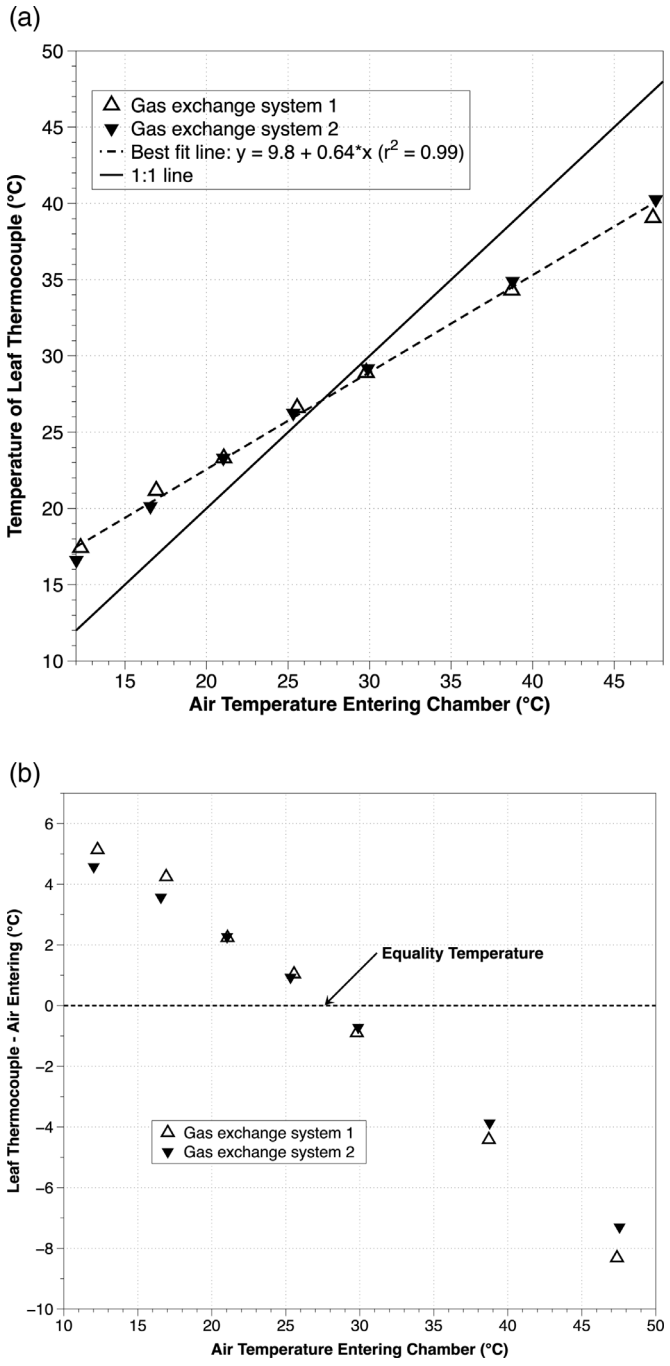

Fig. 2. (a) T_{leaf_m} versus T_{air} as measured in two gas exchange systems with empty cuvettes (open and filled triangles represent different gas exchange instruments). Dashed line is a linear regression model fit of grouped data from both instruments, and the solid line is 1:1. (b) $T_{leaf\_m} - T_{air}$ against T_{air} as measured with empty cuvettes (open and filled triangles represent different gas exchange instruments). The equality temperature occurs where $T_{leaf\_m} = T_{air}$.

interplay among the temperature of the Peltier cooling/heating block (T_{block}), the incoming air temperature (T_{air}), and the temperature of the air at the leaf thermocouple (T_{leaf_m}). When a target block temperature value is set by the operator, sometimes T_{block} is below T_{leaf_m} and sometimes T_{block} is above T_{leaf_m}, depending on the ambient air temperature (T_{amb}) and the flow rate. The Peltier system is effectively competing with the rest of the cuvette surfaces, which seek to equilibrate with T_{amb} as ambient air is being circulated into the cuvette continuously.

The location of each of the temperature measurements in the gas exchange system is also key to understanding the responses shown in Figs. 1 and 2. T_{block} is measured by a thermistor embedded in the block. The block is located directly underneath the fan. T_{air} is measured by a thermistor located in the airstream above the block and below the fan and thus represents air that has already experienced mixing and the influence of T_{block}. Finally, T_{leaf_m} is measured by a thermocouple located in the cuvette immediately below and usually in contact with a leaf. The temperature of the block (T_{block}) influences T_{air} and T_{leaf_m} via air flow through the cuvette which is driven by the internal air pump. Since the thermal conductivity of air is quite low, there will always be a gradient of temperature away from the block; flow rates affect the residence time of air in the cuvette, which will in turn influence the differences among the three temperatures. Therefore, when the block is set below T_{amb}, the following temperature ranking will result: $T_{block} < T_{air} < T_{leaf\_m}$. The opposite ranking will result when T_{block} is set above T_{amb}. The difference in temperature between a leaf (or an empty cuvette) and T_{block} will be dictated by how far from T_{amb} the block is being driven and by the flow rate. As a result of this configuration, as T_{block} is forced further from T_{amb}, the gradient from T_{block} to T_{air} to T_{leaf} will increase.

4. Conclusions

Our findings lead to two general conclusions. First, we show that the behavior of the gas exchange system widely used in studies of leaf gas exchange and temperature dynamics (e.g., Yamori et al., 2014; Slot et al., 2016; Blonder and Michaletz, 2018), produces apparent leaf homeothermy, even when no leaves are in the cuvette. Thus, inferences about aspects of leaf thermoregulation, such as apparent leaf homeothermy, based on gas exchange measurements spanning a wide temperature range, should be made with caution. Second, we caution about the use of similar experimental results when inferring aspects of leaf thermoregulation, energy balance, and controls on leaf transpiration and carbon metabolism, as such experiments necessarily manipulate leaf temperatures well beyond ambient values with consequent potential errors in interpretation.

Here, our data show that the design of the LI-6400 leads to values of T_{leaf_m} and T_{air} which should not be interpreted as representative of leaf-to-air temperature gradients in natural settings. This is particularly important for experimental manipulations which are likely to become more common due to concerns about the impacts of climate warming on plants. We also note that LI-COR explicitly states in its manuals that its leaf thermocouple should not be used to measure T_{leaf} for needleleaf species and other situations in which small leaves or leaflets produce a 3-D structure rather than a planar leaf in contact with the thermocouple. Assuming continuous contact between a given broadleaf and the leaf thermocouple (i.e., T_{leaf_m}), the resulting measurement should yield a valid leaf temperature value. However, because it is often hard to determine if the thermocouple is in full contact with the leaf surface, even for broadleaf species, we recommend that the energy balance calculation (T_{leaf_eb}) be used as a rough check against T_{leaf_m}. Indeed, Mott and Peak (2011) highlighted potential problems in using T_{leaf} measured by thermocouple with a similar gas exchange system to infer aspects of leaf function. In general, however, when chamber temperatures are not forced well above or below ambient T_{air} with broadleaf species (including grasses), T_{leaf_m} should be accurate and representative. Additionally, the new LI-COR 6800 gas exchange uses an insulated thermocouple with exposed wires in contact with the undersides of leaves, presumably in order to avoid having poor thermocouple-leaf contact and chamber air temperature overly influencing T_{leaf_m}, as was shown by Mott and Peak (2011). Other manufacturers use different approaches to measure T_{leaf} that avoid problems introduced by direct contact thermocouple measurements. For example, the iFL gas exchange system (ADC BioScientific Ltd., UK) uses infrared thermometry to measure temperature of the leaf surface, but this approach relies on leaf emissivity which is challenging to determine

independently and can vary with leaf water content (Still et al., 2019). Finally, even the LI-COR leaf energy balance calculation can be problematic when measuring leaf temperature responses far outside the ambient temperature range, given that longwave radiation fluxes required to estimate isothermal net radiation are not measured but are approximated by temperature measurements. In the LI-COR 6400, longwave radiation fluxes are estimated using air temperature measured by the leaf thermocouple (which should be pulled down out of contact with the leaf and ideally shielded from radiative heating when measuring needleleaf species) and wall temperature measured by the airstream thermistor located beneath the air circulation fan. The estimated isothermal net radiation required by the energy balance calculation thus varies non-linearly with the difference between these temperature measurements: as the temperature of the airstream measured by the thermistor beneath the fan exceeds the temperature measured by the leaf thermocouple, the net isothermal radiation increases (and decreases when the opposite temperature gradient occurs).

In addition to potentially misleading ($T_{leaf\_m} - T_{air}$) estimates made by gas exchange systems, we further caution against the use of leaf-chamber experiments to infer leaf temperature dynamics in natural environments. While chamber-based instruments are designed to control environmental conditions that leaves experience, like CO_2 concentrations and relative humidity, these controlled environments do not represent "natural conditions" particularly well. One crucial difference between a cuvette and "real" conditions is the role of the leaf boundary layer in controlling gas exchange and leaf temperature. Air inside a cuvette is well-mixed, specifically to disrupt the leaf boundary layer in order to facilitate a more direct estimate of stomatal conductance. However, boundary layer conductance can limit gas exchange in many plant canopies, particularly those with large leaves and that experience low wind speeds (Roberts et al., 1990; Meinzer et al., 1997; Leigh et al., 2012; Leigh et al., 2017), with significant implications for $T_{leaf} - T_{air}$ differences. Therefore, rather than manipulating the conditions in the cuvette only, exposing the whole plant to the new conditions, and measuring a snap-shot of gas exchange using settings that mimic the ambient conditions as much as possible, would be preferable.

Careful consideration should also be given to any experiment that manipulates air temperature inside the cuvette without consideration of the impact of VPD on g_s and T_{leaf} dynamics, or by experiments that disregard the implicit connections among leaf temperature, stomatal conductance, and plant hydraulic architecture. For example, relative humidity can be maintained in these systems at constant values, but across a suitably large T_{air} range (>10 °C) this can lead to substantial variations in VPD (>2 kPa). Such variations in VPD, irrespective of temperature, would drive large changes in g_s (Oren et al., 1999). A more reliable approach would be to hold VPD - rather than relative humidity - constant. Other considerations for temperature manipulations include the effective length of the hydraulic pathway from the water source. If foliage is measured on an in situ branch, then the natural hydraulic pathway is preserved. However, if branches are cut and placed in water, then unnaturally high transpiration rates with minimal hydraulic consequences might result and bias the interpretation. Finally, the radiation load (from short- and longwave radiation) that a leaf receives in natural settings is quite different from the radiation emitted by a cool LED light source (Nelson and Bugbee, 2015), as is used in most modern gas exchange systems. It is therefore clear that even without the temperature measurement errors introduced by the gas exchange system design, other artificial conditions can limit the usefulness and relevance of temperature response measurements made in gas exchange systems.

Declaration of Competing Interest

None.

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