

Leaf Temperature Effects on Measurements of Diffusive Resistance to Water Vapor Transfer¹

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P. A. MORROW AND R. O. SLATYER

Department of Biological Sciences, Stanford University, Stanford, California 94305 and Department of Environmental Biology, Research School of Biological Sciences, Australian National University, Canberra, Australia

ABSTRACT

Substantial errors can be introduced to estimates of leaf resistance (r_l) obtained from diffusion porometers unless precautions are taken to reduce the leaf-cup temperature difference ($T_{\text{leaf}} - T_{\text{cup}}$) to acceptable levels prior to measurement. When $T_{\text{leaf}} > T_{\text{cup}}$, underestimation of leaf resistance occurs; the reverse applies when $T_{\text{leaf}} < T_{\text{cup}}$.

The effect is most pronounced under open-stomata conditions and declines as stomatal resistance increases. Under typical measurement conditions, $T_{\text{leaf}} - T_{\text{cup}}$ values of the order of 1 C induce a reduction in the ratio of the apparent to true leaf resistance to about 0.8 when the leaf resistance is low ($r_l = 1-2 \text{ sec cm}^{-1}$). When $T_{\text{leaf}} - T_{\text{cup}} = 5 \text{ C}$, the ratio drops below 0.5. Under high leaf resistance conditions ($r_l = 10-50 \text{ sec cm}^{-1}$) the comparable ratios are approximately 0.9 and 0.7, respectively.

During the past few years the water vapor diffusion porometer (1, 4, 8, 9) has become a widely used tool for field studies of stomatal resistance, replacing, to a considerable degree, other types of porometers which measure viscous air flow or some other parameter.

The attraction of the diffusion porometer is that it measures the actual diffusive resistance of the leaf to water vapor movement, and the transfer processes and pathways that are involved are essentially the same as in natural transpiration. These features are not found in other porometers.

Despite these advantages, it is important for users to recognize that the basic calibration and operational procedures for these instruments assume that leaf temperature (T_{leaf}) is the same as porometer temperature (T_{cup}). Many measurements are made on sunlit leaves, under conditions of high radiation and partially or completely closed stomata. Under such conditions T_{leaf} may exceed air temperature (T_{air}) by several degrees (3, 5) and significant errors may be introduced. This paper points out the magnitude of these errors and provides evidence that shading of the leaf prior to measurement, until the assumption that $T_{\text{leaf}} = T_{\text{cup}}$ is acceptable, does not appear to influence stomatal aperture during the measurement period.

Principle of the Method. The instrument consists of a cup, sometimes equipped with internal aspiration, containing a humidity

sensor which is sensitive over a narrow range of relative humidity at the low end of the relative humidity range. In operation, the cup is dried by air from a silica gel dehydrator. It is then placed over the leaf. Transpiration proceeds, the humidity in the cup increases, and the time required for the sensor to respond over a narrow, prescribed (usually 1-2%) range is determined.

Since the relative humidity at the sites of evaporation within the leaf is close to 100% (it is generally assumed to be the saturation vapor pressure at the leaf temperature [7]), and since the humidity sensor is observed over a narrow range at the low end of the relative humidity scale (say, 18-20%), the water vapor concentration difference from leaf to air is assumed to be constant during the period of measurement. Consequently, the transpiration rate (E) can be assumed to be steady during the period of measurement and inversely proportional to the time-lapse (Δt) which occurs as the sensor responds over the measurement range.

Calibration is based on the frequently used transpiration equation:

$$E = \alpha \frac{(e_{\text{leaf}} - e_{\text{cup}})}{r_a + r_l} = \frac{c_{\text{leaf}} - c_{\text{cup}}}{r_a + r_l} \quad (1)$$

where e_{leaf} (mm Hg) is the saturation vapor pressure at T_{leaf} and e_{cup} (mm Hg) is the actual vapor pressure at the mid-point of the measurement range, and at T_{cup} ; c_{leaf} and c_{cup} (g cm^{-3}) are the corresponding water vapor concentrations. The coefficient α converts vapor pressure in mm Hg to water vapor concentration in g cm^{-3} . (It has the value $2.89 \times 10^{-4} e/T$ when T is in degrees Kelvin). The term r_a (sec cm^{-1}) is the diffusive resistance external to the leaf (*i.e.*, of the porometer cup itself) and r_l (sec cm^{-1}) is the diffusive resistance of the leaf.

Since $E = k/\Delta t$, where k is a coefficient of proportionality, this expression can be rewritten as

$$(r_a + r_l)/\Delta t = (c_{\text{leaf}} - c_{\text{cup}})/k \quad (2)$$

At any one level of T_{leaf} and T_{cup} , the right hand side of equation (2) is a constant, so $(r_a + r_l)$ can be uniquely determined, for any one porometer system, by measurements of Δt .

Calibration is generally carried out by determining Δt when the porometer is located over a range of perforated Plexiglas plates, the diffusive resistance of which is calculated from diffusion theory (4). At the base of each plate is a layer of wet blotting paper to simulate the sites of evaporation within the leaf.

Since water vapor must diffuse from the sites of evaporation through the perforations in each plate, and then through the porometer cup to the sensor, the value of Δt obtained from each plate includes a term for the porometer cup resistance, r_a , which is a function of cup geometry. Consequently, the resultant calibration curve of Δt against plate resistance, r_l , really relates Δt to the total diffusive resistance, $(r_a + r_l)$. The value of r_a can be obtained from the negative intercept of the calibration curve on

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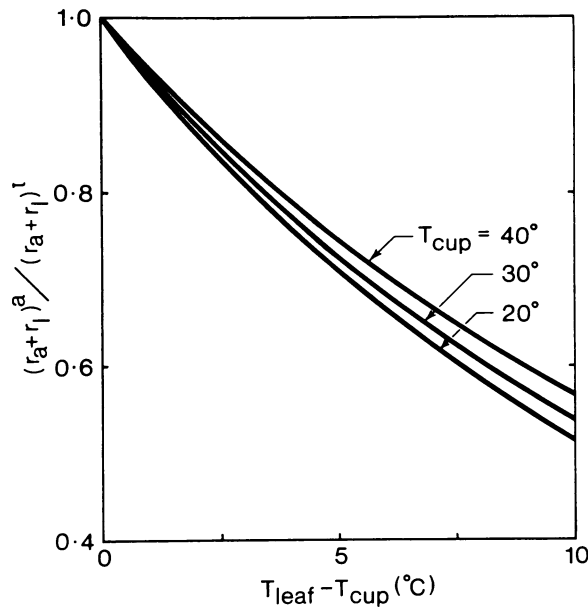


FIG. 1. Effect of differences between leaf and porometer temperature ($T_{\text{leaf}} - T_{\text{cup}}$) on the ratio of the apparent, $(r_a + r_l)^a$, to true, $(r_a + r_l)^t$, total diffusive resistance to water vapor transfer. The three curves refer to different levels of cup temperature.

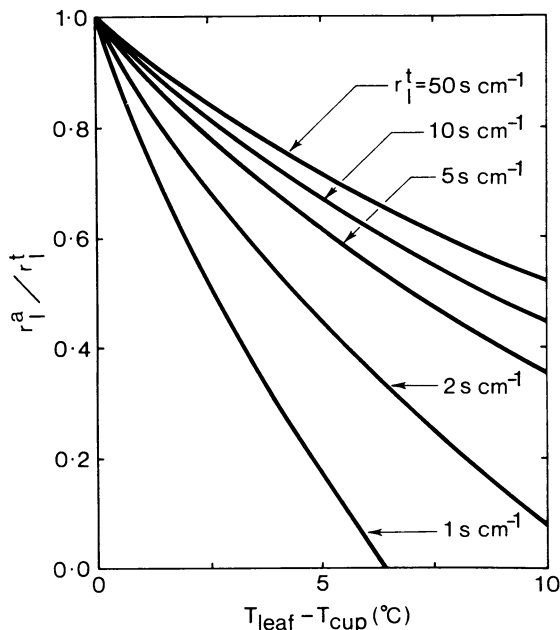


FIG. 2. Effect of differences between leaf and porometer temperature ($T_{\text{leaf}} - T_{\text{cup}}$) on the ratio of the apparent, r_l^a , to true, r_l^t , leaf diffusive resistance to water vapor transfer. The data are for a porometer at 30°C and with an instrument diffusive resistance (r_a) of 2.0 sec cm^{-1} . The five curves refer to actual leaf resistances of 1, 2, 5, 10, and 50 sec cm^{-1} .

the r_l axis. Regardless of whether estimates of r_a are required or not, the calibration provides a valid means of estimating actual r_l values from Δt readings when the porometer is located over leaves.

Effect of Leaf Temperature-Porometer Temperature ($T_{\text{leaf}} - T_{\text{cup}}$) Differences. Calibration curves are generally obtained at several temperatures so that r_l may be calculated from measurements made in the field at different temperatures by interpolation. Theoretical expressions have also been developed to take tem-

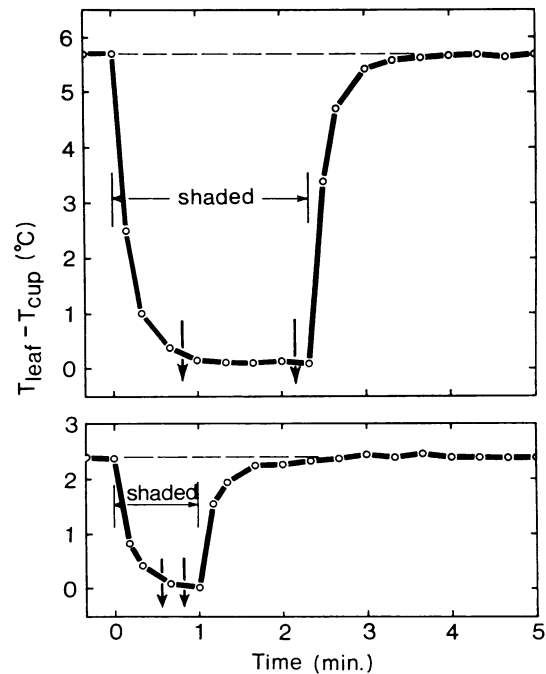


FIG. 3. Time course of leaf-porometer temperature difference ($T_{\text{leaf}} - T_{\text{cup}}$) on *E. pauciflora* leaves in response to a shading treatment. The vertical arrows indicate the beginning and end of the actual porometer measurement. The upper diagram refers to a leaf in which the stomata were nearly closed (high r_l), and the lower diagram to a leaf in which the stomata were open (low r_l). For details see text.

perature into account. Both of these procedures normally assume that, regardless of ambient temperature level, $T_{\text{leaf}} = T_{\text{cup}}$, so that the temperature sensor located in the porometer provides a basis for estimating the term c_{leaf} in equations 1 and 2. Clearly, if $T_{\text{leaf}} \neq T_{\text{cup}}$, this assumption is in error.

The magnitude of this effect can be seen by reference to equation 2. The term $(r_a + r_l)/\Delta t$ refers to the slope of the calibration curve. The ratio of the slope for a given leaf and cup temperature (superscript $'$) to that for a different leaf temperature (superscript $''$) at the same cup temperature, is

$$\frac{(r_a + r_l)/\Delta t'}{(r_a + r_l)/\Delta t''} = \frac{(c_{\text{leaf}}' - c_{\text{cup}}')}{(c_{\text{leaf}}'' - c_{\text{cup}}'')} \quad (3)$$

For any particular stomatal aperture, and hence any $(r_a + r_l)^a$, the ratio of the transit time changes in inverse proportion with changes in the right hand side of equation 3. For any one transit time, therefore, there is an apparent change in the ratio of the total diffusive resistance which is proportional to the changes in the right hand side of equation 3. If $T_{\text{leaf}} > T_{\text{cup}}$, this ratio declines, and so does the apparent value of $(r_a + r_l)$ compared with the true value. The opposite effect occurs if $T_{\text{leaf}} < T_{\text{cup}}$.

These effects are depicted in Figure 1, where the ratio of the "apparent" value of $(r_a + r_l)$ to the "true" value is shown for $T_{\text{leaf}} - T_{\text{cup}}$ differences up to 10°C, and for three levels of cup temperature. The data are based on the assumption that a humidity sensor with a mid-point value at 20% relative humidity is used. If a higher mid-point is adopted the effect is more pro-

² Actually, $(r_a + r_l)$ changes slightly because of a direct effect of temperature on diffusive resistance caused by changes in the diffusion coefficient of water vapor in air. These effects are neglected in this analysis because they are relatively small (<6% for $T_{\text{leaf}} - T_{\text{cup}} = 10^\circ\text{C}$) and do not affect the general interpretations and conclusions which are drawn from the data.

nounced than shown here; a lower mid-point value has the opposite effect. However, most sensors in common use have mid-point values around 20 per cent.

Figure 1 shows that, because of the high degree of dependence of saturation vapor pressure on temperature, $T_{\text{leaf}} - T_{\text{cup}}$ values of about 5 C give apparent values of $(r_a + r_l)$ about 25 to 30% below the true values. If $T_{\text{leaf}} - T_{\text{cup}} = 10$ C under-estimations approaching 50% occur. It is noteworthy that the effects are relatively insensitive to cup temperature itself, increasing only slightly as cup temperature is lowered.

Because values given in Figure 1 include the cup resistance, r_a , they are somewhat conservative in terms of an effect on estimates of stomatal diffusive resistance, r_l . Taking a typical value of 2.0 sec cm^{-1} for r_a , and a cup temperature of 30 C, Figure 2 indicates the effect of a similar range of $T_{\text{leaf}} - T_{\text{cup}}$ values on the ratio of apparent r_l to true r_l , at five different r_l levels, representing open ($r_l = 1.0, 2.0 \text{ sec cm}^{-1}$), partly closed ($r_l = 5, 10 \text{ sec cm}^{-1}$) and closed ($r_l = 50 \text{ sec cm}^{-1}$) stomata.

Figure 2 shows that, when r_l is low, quite small values of $T_{\text{leaf}} - T_{\text{cup}}$, of the order of 1 C, can cause under-estimation of r_l of the order of 20%, and values of 5 C induce estimates of less than half the true value. As the stomata close, however, and the relative magnitude of $r_l/(r_a + r_l)$ increases, the effect becomes less significant. Even at the highest value taken ($r_l = 50 \text{ sec cm}^{-1}$), however, $T_{\text{leaf}} - T_{\text{cup}} = 5$ C causes errors of the order of 30%.

Although leaf temperature is seldom lower than cup temperature, this situation will cause effects in the opposite direction to those shown in Figures 1 and 2.

Recommended Operational Procedure. It is apparent from Figures 1 and 2 that, for most levels of stomatal aperture, measurements of acceptable accuracy ($\pm 10\%$ of the true value) can only be made as long as $(T_{\text{leaf}} - T_{\text{cup}}) < 1.0$ C. Better than $\pm 5\%$ can be achieved if $(T_{\text{leaf}} - T_{\text{cup}}) < 0.5$ C. This is easiest to achieve by the following procedure. First, when not in use the porometer should be kept away from direct sunlight so that $T_{\text{cup}} \approx T_{\text{air}}$. When measurements are required, the leaf should then be shaded until $T_{\text{leaf}} - T_{\text{cup}} < 1$ C. The porometer should then be attached to the leaf and the measurement carried out. (The alternative procedure of attempting to change T_{cup} , until this condition is met, is very difficult to achieve, and separate measurement of T_{leaf} and T_{cup} introduces unnecessary complications since separate calibration curves would be required for various combinations of T_{leaf} and T_{cup} .)

The main problem introduced by shading is the possibility that there may be a change in stomatal aperture, and hence in r_l , before the measurement is completed. In order to check on this, leaves from species of *Eucalyptus*, *Atriplex*, and *Arbutus* were arranged under a constant light source which provided an energy load approximately equivalent to full sunlight, and a fan was directed across the leaf surface to provide a reasonable rate of air movement. A thermistor was clipped on to the leaf and $\Delta T = (T_{\text{leaf}} - T_{\text{cup}})$ monitored. When conditions steadied, the leaf was shaded until $\Delta T < 1$ C. The porometer was then located on the shaded leaf and a measurement carried out. At the conclusion of the measurement both the porometer and shading treatment

were removed. The entire procedure was repeated 10 minutes later.

Typical results from *Eucalyptus pauciflora*, plotted in Figure 3, clearly show that ΔT falls to acceptable levels within 30 sec of imposed shading, is maintained at < 0.5 C during measurement, and then returns to a level close to its original value when shading is removed. The same pattern was observed when the experiment was repeated.

Had there been any change in stomatal aperture following the shading treatment, this would have been reflected in the steady state, illuminated values at ΔT , since all other components of the energy balance were constant (2, 7).

In consequence, the shading treatment appears to be an effective way of ensuring reliable measurements, at least for the species and conditions examined here.

It is possible that with more sensitive species, or under different conditions, more rapid changes in aperture may be observed. Should changes occur during the period of shading, it is clear that this procedure would be unacceptable and the porometer technique itself inappropriate. It is therefore most important to check stomatal responsiveness to shading prior to measurement. Fortunately situations favoring rapid response are likely to be associated with wide open stomata and nonstress conditions, in which ΔT would be low prior to shading, relatively brief shading would be sufficient to reduce it to acceptable levels, and the porometer measurement itself would be relatively rapid.

The water vapor diffusion porometer provides an inexpensive, easily used tool for the measurement of an ecologically and physiologically important plant parameter. However, factors other than leaf-cup temperature difference may also affect its performance and reliability. These include the degree of sensor dehydration which is imposed prior to each measurement, drift in the sensor response during a measurement, drift in the calibration curve obtained for any one temperature, and the degree of temperature dependence of the calibration curve. These factors are considered in a separate communication (6).

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