Sources of Error in the Estimation of Stomatal Conductance and Transpiration from Porometer Data

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Stomatal control of leaf conductance is an important means by which plants limit water loss. It is often used as an indicator of water stress, and it is an important factor in photosynthesis studies. Automated commercially available equipment for measuring leaf conductance has become available in recent years from several manufacturers. When properly used, this equipment makes it easy to obtain reliable field measurements. However, if the instruments are not used or calibrated properly, they can give conductance estimates that appear "reasonable," and yet are in significant error.

The purpose of this paper is to describe a) the effects of sensor or calibration errors on the accuracy of conductance measurements, b) the relationship between molar conductance units that are coming into prominent use and velocity units that are used in the older literature, and c) some considerations that will help protect the quality of porometer data. This discussion is limited to porometry as it relates to water vapor exchange. Up-to-date general reviews of instrumentation and procedures for gas exchange measurements can be found in Coombs et al. (1985), Field et al. (1989), Parkinson (1985b), and Percy et al. (1989). Sestak et al. (1971) provides an exhaustive review of literature and methods up to 1971.

Porometers in general use today fall into two broad categories, transient or steady state, according to the measurement principle on which they are based. Transient porometers may be ventilated, in which a fan provides rapid chamber mixing, or unventilated, in which cuvette humidity changes occur strictly by diffusion. In ventilated transient porometers (Komer and Cernusca, 1976; Tan and Black, 1978; Turner and Parlange, 1970), stomatal resistance is calculated from the rate and magnitude of change in cuvette humidity, and system volume. In unventilated transient porometers (van Bavel et al., 1965; Kanemasu et al., 1969; Monteith and Bull, 1970; Stiles, 1970; Visscher, et al., 1978), resistance is not computed directly from the magnitude of changes in relative humidity. Instead, a measured transit time is compared to an empirical calibration curve that relates diffusion path length to measured transit time. The transit time is determined by leaf resistance, sensor geometry, and temperature.

The porometer constructed by Stiles (1970), and theoretically described by Monteith and Bull (1970) is the basis of a modern commercially available transit-time porometer (Delta-T Mk III, Delta-T Devices, Cambridge, U.K.). A calibration plate containing a series of pore fields with resistances known from diffusion theory is provided by the manufacturer. A plot of resistance vs. transit time is constructed using the calibration plate at field temperature, and compared to measured leaf transit times.

The advantages of this system are: a) accurate absolute calibration of the RH sensor is not required; b) the empirical calibration procedure is easy; and c) stomatal responses that are related to altered boundary layer conductance may be less serious with the unventilated porometer than with the ventilated type. However, the calibration is temperature dependent, so it must be performed frequently when ambient temperature changes; also, resistance is known only after recourse to a standard calibration curve. Detailed general error analyses for this system have appeared (Gay, 1983; Monteith and Bull, 1970; Monteith et al., 1988), so transit-time porometers will not be considered further here.

Four types of ventilated porometers will be considered: these include the flow-through steady state porometer, automatic null-balance steady state porometer, and ventilated transient porometer; the fourth type, a recirculating manually controlled null-balance porometer has some of the characteristics of each of the first three types. Diagrams showing the essential features of each system and the equations used to compute conductance in each are given in Fig. 1 A-D.

The purpose of this discussion is to show how various kinds of practical calibration and operational problems can affect conductance measurements, not to present a detailed discussion of gas exchange calculations. Therefore, the simplest possible description for each of the systems is used, and various considerations that enter into modern gas exchange calculations have been omitted. Phenomena, such as the convective effects of water vapor flux in stomatal pores, are described thoroughly elsewhere (Ball, 1987; Farquhar and Sharkey, 1982; Jarman, 1974; Leuning, 1983; von Caemmerer and Farquhar, 1981), and their omission will not affect the conclusions drawn here.

The chamber arrangement of a flow-through steady state system is shown in Fig. 1A. Air of known vapor pressure enters the leaf chamber where it accumulates moisture due to transpiration by the leaf. Rapid mixing is provided by a fan, so chamber air and the exit airstream are assumed to have the same vapor pressure. When the chamber vapor pressure is constant, leaf conductance is computed from the air flow rate, the vapor pressure of inlet and outlet airstreams, the saturation vapor pressure at leaf temperature, and from leaf area. The ADC LCA (Analytical Development Corp., Hoddeson, Herts, U.K.) is a commercially available instrument using this measurement principle. The ADC system also measures the CO₂ exchange rate, and the system flow rate is set to give an appropriate CO₂ differential between the inlet and outlet airstreams. The chamber relative humidity comes to different steady state values as the flow rate is varied to accommodate various CO₂ exchange rates.

The chamber arrangement of a null-balance steady state porometer is shown in Figure 1B. A relative humidity (RH) set-point,

The author wishes to thank J.T. Ball, T.M. De Jong, J.M. Norman, and J.M. Welles for critical readings of early versions of the manuscript and for many helpful suggestions.

Fig. 1. (A) Chamber arrangement describing a flow-through steady state system. Leaf conductance is computed according to

$$g_L = \frac{u}{s} \frac{e - e_i}{\Delta e},$$

where u is flow rate ($\text{mol}\cdot\text{s}^{-1}$), s is leaf surface area (m^2), e is chamber and outlet air vapor pressure (Pa or kPa), e_i is inlet air vapor pressure (Pa or kPa), and Δe is the leaf-to-air vapor pressure difference [$= e^*(T_L) - e$, Pa or kPa]; T_L is leaf temperature (K). Vapor pressure can be calculated as $e = \text{RH} [e^*(T)]/100\%$, where RH is the measured relative humidity, T is air temperature, and $e^*(T)$ is the saturation vapor pressure at temperature T that can be obtained from appropriate formulae [e.g., Buck (1981), Lowe (1977)] or tables [List (1984)]. (B) Chamber arrangement showing an automatic null-balance steady state porometer in which chamber relative humidity controls the system flow rate in such a way that a pre-set relative humidity is maintained. Conductance is computed according to

$$g_L = \frac{u}{s} \frac{e}{\Delta e}$$

Symbols are described at Fig. 1A. (C) Chamber arrangement showing a transient ventilated porometer. Conductance is computed according to

$$g_L = \frac{V\rho}{s} \frac{1}{\Delta e} \frac{de}{dt},$$

where V is the chamber volume (m^3), ρ is the mole density of chamber air ($= P/RT$, $\text{mol}\cdot\text{m}^{-3}$), R is the gas constant ($= 8.314 \text{ m}^3 \text{ Pa}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$), and de/dt is the chamber vapor pressure rate of change that is computed from relative humidity and temperature. Other symbols are described at Figure 1a. (D) Chamber arrangement showing a manually controlled null-balance porometer that can be operated in either transient or steady state mode, or a combination of the two. Conductance is computed according to

$$g_L = \frac{V\rho}{s} \frac{1}{\Delta e} \frac{de}{dt} + \frac{u_d}{s} \frac{e}{\Delta e}$$

where u_d is flow rate through the desiccant ($\text{mol}\cdot\text{s}^{-1}$). Other symbols are defined at Fig. A and C.

usually ambient RH, is entered into the instrument. When a leaf is enclosed in the chamber, the humidity begins to rise, and a flow of dry air that is sufficient to bring the relative humidity back to the set point and maintain it there, thus balancing leaf transpiration, is supplied to the chamber. Leaf conductance is computed from the dry air flow rate, chamber vapor pressure, leaf saturation vapor pressure, and leaf area. A good desiccant is required to provide dry input air. The LI-1600 (LI-COR, Lincoln, Neb.) is a commercially available instrument of this type.

The chamber arrangement of a transient ventilated porometer is shown in Fig. 1C. When a leaf is enclosed in a porometer of this type, the humidity begins to rise as transpiration adds water vapor to the system. Leaf conductance is computed from the vapor pressure change rate, system volume, leaf saturation vapor pressure, and leaf area.

A purely transient system does not require a flow rate measurement or a good desiccant, but it does require an accurate measure of system volume. Measurement of this simple characteristic is complicated by water sorption. Early porometer designers recognized this problem and used various methods to estimate an apparent system volume to account for water sorption. Total apparent volumes for published systems vary from 1.4 times geometric volume for a porometer with a Vaisala HUMICAP humidity sensor (Visscher et al., 1978), up to several times the geometric volume for porometers using strongly hygroscopic LiCl sensors (Körner and Cernusca, 1976; Tan and Black, 1978; Turner and Parlange, 1970). Water sorption is strongly temperature dependent, so apparent volumes decrease toward geometric volume as temperature increases (Tan and Black, 1978; Visscher et al., 1978). No purely transient ventilated porometers are commercially available.

An intermediate between the transient porometer and the steady-state porometer is represented by the LI-6200 (LI-COR). The LI-6200 (Fig. 1D) is a closed loop system in which a portion of the airstream is dried, remixed with the remaining moist air in the loop, and then returned to the chamber. Relative humidity can be made to increase, decrease, or remain the same, so it can be operated in steady-state or transient mode. In practice, the RH usually changes slightly during a measurement, so conductance has both a steady-state component dependent on flow rate, and a transient component dependent on vapor pressure rate of change and volume; but the steady-state term is usually predominant. The LI-6200 has a simple test and software provision to measure a parameter called K_{abs} , which multiplies the transient term and corrects for water sorption. K_{abs} has been found to vary between ≈ 1.1 and 1.5, depending on the chamber used and measurement conditions. This value is equivalent to the variable system volume reported by earlier porometer designers. In contrast to water vapor, the CO_2 exchange rate is measured entirely in transient mode in the LI-6200.

GENERAL TECHNIQUE

Desiccant

Null-balance porometers and some flow-through porometers require dry input air. In portable systems, the dry air source is usually provided by passing ambient air through a desiccant, and the humidity of the incoming air is then assumed to be at or near zero. It is essential in such systems that desiccant be checked often when many measurements are being made and changed or regenerated (as the case may be) at least daily. The conductance error that results when incoming air is 1% to 3% RH higher than assumed is shown in Fig. 2. If the incoming air has a nominal humidity of 0%, the x-axis can be considered as the chamber RH; otherwise, it is the difference between the chamber RH and the RH of the incoming air. In a null-balance system operating at a chamber RH of 30% to 60%, incoming air that is 3% RH instead of 0% RH will cause a conductance error of $\approx 5\%$ to 11%.

Many porometers use magnesium perchlorate or silica gel as desiccants. Anhydrous magnesium perchlorate in a LI-COR S-cm drying tube three-fourths full (actual desiccant volume $\approx 11 \text{ cm}^3$) will maintain the output RH at or below 1% for almost 3 hr when presented with a continuous flow of moist air (RH = 74%) at 1 liter·min⁻¹ and 25C. Output RH increases sharply when magnesium perchlorate saturates. Freshly regenerated silica gel (175C for 1 hr) in a LI-COR 10-cm drying tube (desiccant volume $\approx 25 \text{ cm}^3$) will maintain the output RH at or below 1% for >4 hr under similar conditions; but the RH increases gradually when silica gel begins to saturate, so errors may occur unnoticed.

Fig. 2. Relative error in conductance arising from incoming leaf chamber air having a relative humidity of 1% ($\square$), 2% ($+$) or 3% ($\diamond$), when dry air is expected. Data are plotted as a function of chamber fractional humidity (= relative humidity (%) / 100%). ($\Delta g/g = (h_i - h_e) / (h - h_i)$), where h_i = actual incoming humidity, h_e = expected incoming humidity, h = chamber humidity.]

Even a 1% error in estimated incoming RH can cause substantial conductance errors in a steady-state system where the incoming air can be far from zero and the RH difference between chamber and incoming air $<20\%$. For this reason, Schulze et al. (1982) found that a Vaisala HUMICAP was not sufficiently accurate to measure the humidity increase caused by a leaf in an open system under nonisothermal conditions. Instead, they used a differential water vapor analyzer to measure the humidity difference between chamber inlet and outlet air, and the HUMICAP to estimate the chamber RH needed to calculate the leaf-to-air vapor pressure difference (VPD).

Chamber temperature

The temperature of a leaf enclosed in a porometer cuvette often increases during a conductance measurement. One of the main drivers for such increases is chamber wall temperature. Leaf temperature increases can be reduced by keeping the porometer cuvette open and in the shade, with the fans running, between measurements.

In evaluating the LI-1600 sensor head, Schulze et al. (1982) found a 0.3C increase in cuvette air temperature over ambient air temperature due to the presence of a mixing fan in the cuvette. Measurements made over a period of minutes in full sun ($800 \text{ W} \cdot \text{m}^{-2}$) in the central Sahara produced cuvette air temperatures that were $\approx 1.2\text{C}$ above ambient. After several hours of continuous use in full sun, a maximum cuvette temperature 3.5C above air temperature was reported.

Thin-walled transparent chambers made of polycarbonate, such as those used in the LI-6200, exchange heat very quickly with the surroundings; however, it is still important to keep them shaded when not in use. If individual measurements that require tens of minutes are to be made in full sun (e.g., CO_2 response curves), leaf temperature increases can be greatly moderated by using an external fan to pass ambient air around the outside of the chamber. For example, when a big blue stem (*Andropogon gerardii* Vitman) leaf of $\approx 5 \text{ cm}^2$ was enclosed in a 250 ml chamber at an outside air temperature of $\approx 40\text{C}$, the chamber air remained near 41C with an external fan, whereas it gradually increased to 44C without the fan (J.M. Norman, personal communication).

A one-fourth-inch Plexiglas filter does a good job of removing long-wave radiation under greenhouse or growth chamber conditions with high intensity discharge (HID) lamps. We found that in the presence of external air movement, these inexpensive filters virtually eliminated temperature increases in soybean leaves at 28C when the VPD was 2.2 kPa and light intensity was $1.3 \text{ mmol quanta s}^{-1} \cdot \text{m}^{-2}$. However, neither Plexiglas nor near-infrared filters, such as the Schott KG-4, are of much use in the field (J.M. Norman, personal communication). This is not surprising because leaf absorptance is small from 700 to 1400 nm where the solar spectrum still provides substantial radiant energy; and beyond that range, leaf absorptance increases, but the proportion of energy remaining in the solar spectrum is small (Gates, 1980). By contrast, $\approx 40\%$ of the radiant energy from HID lamps is in the thermal range beyond 2500 nm (Jack and Koedam, 1974) where Plexiglas absorbs.

Chamber cleanliness

Nearly all types of debris that accumulate in porometer cuvettes will serve as sources or sinks for water vapor. Any hygroscopic debris as well as the cuvette surfaces will sorb or desorb water vapor if the cuvette humidity is displaced from equilibrium with ambient conditions; this occurrence will slow the return to equilibrium and lengthen the system response time. This delay can be a problem even in a steady-state system if it is important to make a measurement quickly ($<60 \text{ sec}$) to minimize changes in stomatal aperture. However, water sorption will have no effect on the final results if the system returns to a steady-state condition.

The problem is more serious in a system such as the LI-6200 that permits photosynthesis and conductance measurements while relative humidity is changing. Transpiration is computed from the sum of a steady-state term and a transient term. The rate of change in vapor pressure (computed from RH) will always be an underestimate in the presence of water vapor sorption. If humidity is increasing, hygroscopic surfaces in the chamber will take up water

vapor, slowing the increase; and if humidity is decreasing, then water vapor will be released, slowing the decrease. A simple test that measures water vapor sorption is available with the LI-6200, and a correction on the transient term is included in the software.

CALIBRATION

Equations used to compute conductance for each of the systems described in Fig. 1 A-D are given in the figure legends. Conductance errors arising from a measurement error in one of the variables (5) in those equations can be evaluated from

where $\Delta g/g_L$ is the relative change in leaf conductance for a given change, $\Delta \xi$ in variable (or sensor) ξ (Campbell, 1975). In all cases, vapor pressures are converted to fractional humidities ($= RH/100\%$) as the last step, and results are plotted as functions of measured fractional humidity. Equations plotted in the figures are given in the figure legends. When both input air and chamber air are part of an analysis, their temperatures are assumed equal for purposes of calculation.

Relative humidity

Data accumulated on 92 LI-1600s returned to LI-COR for calibration over a recent 12-month period give some indication of the magnitudes of relative humidity errors that are commonly made. When the instruments are returned, measurements are made on air at three known relative humidities before calibration, and again after calibration. Results before calibration are shown in Fig. 3. Many of the sensors are in very serious error. Considering all three RH levels, $\approx 26\%$ of the measurements are in error by more than $\pm 10\%$ RH at one or more of the RH levels. Twenty-one percent of the measurements are within the $\pm 3\%$ RH accuracy of the factory specification at all RH levels, and the remainder fall somewhere in between. The sensors read low in most cases.

Linearity of the HUMICAP is about $\pm 1\%$ from 0% to 80% RH. A plot of the typical sensor deviation expected over the full range of RH values is shown in Fig. 4. Calibration of the LI-1600 involves a zero and span adjustment, and is therefore a compromise. The LI-6200 uses a zero and span adjustment plus a software calibration table to correct for sensor nonlinearity.

It is clear from the previous discussion that errors in RH measurement can be large, and are probably frequent. The effect on conductance of a 2% RH measurement error as it varies with chamber fractional humidity ($= RH/100\%$) is shown in Fig. 5. Data are given for two air temperatures and for the leaf assumed cooler than, equal to, or warmer than air temperature. The data in Fig. 5 pertain to a steady-state system in which the incoming air is assumed to be at 0% RH. This would be the case in a null-balance porometer such as the LI-1600, in a system such as the LI-6200 where only the dry air flow rate is measured and the relative humidity can be held constant, and in the ADC LCA-Z steady-state system in its usual operating mode.

The fractional error in conductance due to a 2% error in RH is a strong function of chamber relative humidity. Even small errors in humidity measurements can lead to large errors in conductance when chamber humidity is either very low or very high.

The effect of a relative humidity offset has little dependence on air temperature alone, but it varies strongly with the difference between air and leaf temperatures. The sharp increase in error at high humidity occurs because the leaf to air VPD occurs in the denominator of the error equation. If leaf and air temperatures are the same (regardless of their absolute values), then at an air relative humidity of 100%, the VPD becomes zero, and the error in conductance goes to infinity. But if the leaf is warmer than the air, then the saturation vapor pressure of the leaf will always be higher than that of the air. It follows that even when relative humidity of the air approaches 100%, the VPD can never go to zero, and the conductance error is moderated.

Conversely, if the leaf is cooler than air, then the VPD becomes zero at air relative humidities $< 100\%$ because the saturation vapor

Fig. 3. Measured relative humidity (RH) minus actual RH for 92 LI-1600 porometers returned to LI-COR for recalibration over a recent 12-month period. After recalibration, all of the instruments were well within factory specifications ($\pm 3\%$ from 0% to 80% RH).

Fig. 4. Measurement error as a function of relative humidity for a typical fully calibrated Vaisala HUMICAP relative humidity sensor.

Fig. 5. Relative conductance error resulting from a 2% humidity offset in a null-balance steady state system. Data are presumed for two air temperatures, and for leaf temperature warmer than, equal to, or cooler than air. Air temperature 20C: leaf temperature 18C ($\square$), 20C ($+$), and 22C ($\diamond$). Air temperature 40C: leaf temperature 37C (Δ), 40C ($\times$), and 43C (∇). When leaf temperature equals air temperature the 20C curve and 40C curve coincide. $[\Delta g/g = \Delta h/(h - h_s) + \Delta h/(r - h)]$, where Δh = relative humidity offset (2%), and $r = c^*(T_L)/c^*(T)$, the ratio of saturation vapor pressure at leaf temperature to saturation vapor pressure at air temperature.]

pressure of the leaf is lower than that of the air; thus, the conductance error increases sharply at lower relative humidity values. However, the practical consequences of this observation are reduced because energy balance considerations make it unlikely that leaf temperature will be lower than air temperature when the VPD is small, at least in bright light. In dim light, both stomatal conductance and transpiration are often low so leaf temperature is still not expected to be very much lower than air temperature.

The large increase in error at low relative humidities occurs because a 2% offset becomes an increasing proportion of the chamber humidity as the chamber humidity declines toward zero; and the error term $\Delta h/h$ approaches infinity as chamber relative humidity approaches zero. This result is similar to the effects of bad desiccant discussed earlier.

A similar error analysis for a transient system is shown in Fig. 6. Here it is assumed that conductance is computed from measurements of the change in chamber relative humidity (or vapor pressure), leaf temperature, and air temperature. (This figure does not apply to the empirically calibrated transient porometers discussed earlier.) The LI-6200 uses such an equation when the relative humidity is not held constant. A transient measurement of conductance is subject to much less error at low relative humidities than is a steady-state measurement. But this advantage may be offset by water sorption errors that occur when relative humidity changes.

Many gas exchange systems use a mixing device or dewpoint generator to provide a fixed and "known" relative humidity to the chamber (Bail, 1987; Field et al., 1989). The transpiration rate is calculated from the difference between the chamber humidity and the incoming humidity, and from the flow rate. The upper set of curves in Fig. 7 shows conductance error vs. chamber relative humidity for such a system when the incoming relative humidity is considered perfectly known and fixed at 10%, and a 2% RH offset is assumed in the chamber RH measurement. The upper error curves look like those in Fig. 5 except the lower limit is now 40% RH instead of 0% RH. This change has the effect of greatly increasing the sensitivity of conductance measurements to relative humidity measurement errors, and it indicates an optimum relative humidity range in which errors can be minimized.

The conductance error resulting from a 2% RH offset is reduced if the relative humidity of the incoming and outgoing air is measured with the same sensor or with matched sensors (Fig. 7, dashed curves). The sharp error increase observed earlier when the difference between incoming and outgoing air was small, does not appear because a 2% offset occurs in both measurements. If the RH measurement errors are pure offsets, they will cancel; if they are proportional to the reading (span drift), the resulting conductance error will be somewhat larger than shown in Fig. 7. In any case, the contrast between these two models provides ample motivation to either use the same sensor to measure incoming and outgoing air (e.g., a differential water analyzer) or to be careful in matching the

Fig. 6. Relative conductance error resulting from a 2% humidity offset in a transient system. Temperatures and symbols as in Fig. 4. $\Delta g/g = \Delta h/(r - h)$.

chamber RH sensor with whatever source or sensor is being used to set or measure the incoming relative humidity.

These considerations have some practical consequences. The first pertains to relative humidity sensor calibration. While small span shifts do occur, the largest sensor calibration shifts are zero offsets [Fig. 3; Percy et al. (1989)]. Offset shifts can be detected by doing simple calibration checks on a daily basis. Zero offsets can be detected by reducing chamber RH with desiccant that is known to be fresh; the chamber RH should be within 2% of zero. Sensor span can be checked by exhaling three times or so into the leaf chamber when there is no dry air flow; the span RH should be $\approx 96\%$. Ambient relative humidity can be checked by appropriate comparison with a dewpoint hygrometer or an aspirated psychrometer. These are not calibrations, of course, but they will detect serious errors.

Relative humidity sensors should be carefully calibrated at least once a year or more often as test results dictate. A laboratory calibration should be performed using a dewpoint hygrometer, a water bath dewpoint system, a salt cup system using the variation in equilibrium relative humidity over saturated salt solutions (LI-COR), or other dewpoint generating systems such as the ADC Water Vapor Generator Model WG 600 if a factory calibration is not readily available.

If conductance measurements are to be made at high relative humidities, expect better results when leaf temperatures are above air temperature than when they are below air temperature. When leaves are in full sun and humid air, leaf temperatures above air temperature can be expected and conductance measurements can be made with reasonable accuracy. However, in an understory, humidity can be high and light intensity low, so leaf temperatures are likely to be near or slightly below air temperature. In those cases, it will be more difficult to make accurate conductance measurements.

Some characteristics of the Vaisala HUMICAP compound the difficulties in making measurements at high relative humidity. The HUMICAP has a fast response time and works very well in the range 0% to 80% RH; however, at high relative humidities (especially $>90\%$) its response time is reduced, hysteresis occurs over repeated drying cycles, and reduced accuracy can be expected (Percy et al., 1989; Salasmaa, 1986). If the sensor is stored at high relative humidities, calibration shifts will occur. These problems are important because they occur under precisely those conditions where small humidity measurement errors cause large errors in estimated

Fig. 7. Relative conductance error resulting from a 2% humidity offset in a flow-through steady state system. Solid curves: humidity of incoming air measured or set with assumed perfect accuracy to 40% RH, and chamber RH measured independently with an offset of 2%. Dashed curves: incoming air and chamber air measured with the same sensor, or with perfectly matched sensors. Air temperature 18°C. Leaf temperature 18°C, 20°C, or 22°C. $[\Delta g/g = (\Delta h - \Delta h_i)/(h - h_i) + \Delta h/(r - h)]$. When incoming air is known without error, $\Delta h_i = 0$ (solid curves). When sensors are perfectly matched with only an offset error, $\Delta h = \Delta h_i$ (dashed curves). Δh_i is error in estimated humidity of incoming air.

conductance. Some of the special problems associated with gas exchange measurements in the humid tropics are discussed by Pearcy et al. (1989) and Field (1984).

Air temperature

The effects on conductance of a 0.5C offset in air temperature are shown in Fig. 8 for transient, null-balance steady-state and flow-through steady-state porometers. Only the fractional humidity range from 0.4 to 1 is shown because it is assumed again that the incoming humidity of the flow-through system is 40%, and the errors in the other two systems only continue to decline to below 0.1% as chamber humidity drops toward zero. In both the transient and null-balance steady-state porometers, a 0.5C error in air temperature affects the conductance measurement by < 1% up to ≈80% RH. As will be shown later, these results are scarcely affected by changes in air temperature. The error is much larger with the flow-through system when the difference between the relative humidity of the incoming air and chamber air is small, and the error increases with all the systems when the difference between chamber relative humidity and water vapor saturation is small, i.e., at high chamber humidities.

Conductance is relatively insensitive to errors in air temperature; however, many systems use an air temperature thermistor for the leaf temperature thermocouple reference junction. Thus, an air temperature offset translates into a comparable leaf temperature offset, which, in turn, will cause a sizable conductance error, as is shown in the next section.

Leaf temperature

Conductance calculated for each of the systems has the same functional dependence on leaf temperature, so a leaf temperature offset affects them similarly. Effects of a 0.5C leaf temperature offset at 20, 30, and 40C when leaf and air temperatures are equal, and at 30C when the leaf is either 2C warmer or 2C cooler than air are shown in Fig. 9.

Note that the conductance error scale is 10 times larger than the air temperature error scale. The relationship describing leaf temperature error for all three systems has the same form as that describing air temperature error for the null-balance system, except that it is multiplied by λ/RT_L (λ = latent heat of vaporization of water = $43.7 \text{ kJ} \cdot \text{mol}^{-1}$ at 30C) and it is opposite in sign. The additional factor appears because of the highly temperature-dependent phase change from liquid water to water vapor that occurs in the leaf, and which causes the measured conductance to be ≈17 times more sensitive to an error in leaf temperature than to an error in air temperature.

The similarity of the 20, 30, and 40C curves shows there is very little conductance error dependence on leaf temperature magnitude when leaf and air temperatures are equal. That is also true when leaf and air temperatures are not equal; however, the difference between leaf temperature and air temperature is important, especially at higher humidities. Errors are smaller when the leaf is warmer than air, and larger when leaves are cooler than air for the same reasons described for humidity, i.e., the error term is multiplied by the inverse of VPD. Low leaf temperatures reduce the VPD at all humidities, and they have the largest effect when humidities are high.

These considerations have some practical consequences. Small leaf temperature offsets have a large effect on conductance, so leaf temperature should be measured carefully. Leaf temperatures are usually measured with a thermocouple that uses an air temperature thermistor or similar device as a reference junction. The thermocouple and reference thermistor must be matched, i.e., they should read the same value when measuring the same temperature. Both the LI-1600 and the LI-6200 have ready provision to do this. Good contact must be made between the thermocouple and the leaf.

Leaf thermocouples usually underestimate the temperature difference between leaf and air due to convection and heat conduction along the thermocouple wires. Ziegler-Jons et al. (1986) discuss this problem and give a simple calibration model to make an appropriate correction.

Fig. 8. Relative conductance error resulting from a 0.5C offset in air temperature. Air temperature and leaf temperature both assumed to be 30C: flow-through steady state system ($\diamond$); null-balance steady state system (+); transient system ($\square$). [Flow-through: $\Delta g/g = [h/(r-h)][(r-h_1)/(h-h_1)]\Delta T/T$; null-balance: $\Delta g/g = [r/(r-h)]\Delta T/T$; transient: $\Delta g/g = [h/(r-h)]\Delta T/T$.]

Fig. 9. Absolute value of relative conductance error resulting from a 0.5C leaf temperature offset. Middle three curves: air temperature and leaf temperature equal, where air temperature is 20C ($\square$), 30C (+), or 40C ($\times$). Upper curve ($\diamond$): air temperature is 30C, leaf temperature is 28C. Lower curve ($\triangle$): air temperature is 30C, leaf temperature is 32C. [$-\Delta g/g = [r/(r-h)][\Delta T_L/T_L][\lambda/l]$ where T_L is leaf temperature. $|\Delta g/g|$ is plotted.]

Flow meter

Some electronic flow meters are quite temperature sensitive, so the flow meter zero offset must be adjusted by the user. For example, the LI-6200 has a simple software routine for setting the flow meter zero, but no offset adjustment is routinely required on the LI-1600 or LI-6000. If your system requires a routine zero adjustment, check it regularly. The relative conductance error resulting from a flow meter offset (Δu , $\text{mol} \cdot \text{s}^{-1}$) or calibration error is given by $\Delta u/u$, where u is flow rate ($\text{mol} \cdot \text{s}^{-1}$). Low flow rates are usually associated with low transpiration rates; and when flow rates are low, serious conductance errors—even negative conductances—can result from small zero offsets. With high flow rates, conductance errors resulting from flow meter offset errors will be smaller.

A WORD ABOUT UNITS

Two unit systems for expressing conductance are in wide use today. If telephone calls received are any indication, there is some uncertainty about the relationship between them and the advantages, if any, of one over the other. In the older system, transpiration is usually expressed in terms of a water vapor density gradient between

leaf and air, and conductance is expressed in units of velocity, e.g. $\text{m}\cdot\text{s}^{-1}$, $\text{cm}\cdot\text{s}^{-1}$, etc. (Hall, 1982; Nobel, 1984); these units will be referred to as velocity or conventional units.

In the newer system, transpiration is expressed in terms of a water vapor mole fraction gradient between leaf and air, and conductance has units of mole flux, i.e., $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. These will be called mole conductance units (Incoll, 1985). The present discussion will be simplified without loss of generality by considering one-sided, total leaf conductance. Air density will be expressed as ρ ($\text{mol}\cdot\text{m}^{-3}$). Water vapor density in chamber air will be expressed as ρ_w ($\text{mol}\cdot\text{m}^{-3}$), and leaf water vapor density as ρ_{wL} . In general, variables that pertain to the leaf will be given the subscript L, and variables that pertain to chamber air will have no additional subscript.

In the velocity unit system,

$$E = g_v(\rho_{wL} - \rho_w), \quad [2]$$

where g_v is conductance in velocity units ($\text{m}\cdot\text{s}^{-1}$), and $\Delta\rho_w$ is the leaf-to-air water vapor density gradient ($\text{mol}\cdot\text{m}^{-3}$). Conductance can be described by

$$g_v = \frac{D}{L_s + L_b}, \quad [3]$$

where D is the diffusion coefficient for water vapor in air ($\text{m}^2\cdot\text{s}^{-1}$), and L_s and L_b are equivalent pathlengths (m) for stomata and boundary layer, respectively (Cowan, 1977). Combination of Eqs. [2] and [3] gives an alternative statement of Fick's first law of diffusion in finite difference form ($J = -D\Delta c/\Delta x$). The pathlength L_s expresses the effective depth of the stomatal pore times the fraction of total leaf area occupied by the open stomata, and L_b expresses the effective thickness of the unstirred air boundary layer (Nobel, 1984). The combined diffusion pathlength defined in Eq. [3] is 2.5 mm for a leaf with a conductance of $0.01 \text{ m}\cdot\text{s}^{-1}$ and a water vapor diffusion coefficient of $2.5 \times 10^{-5} \text{ m}^2\cdot\text{s}^{-1}$ at 20°C .

In the mole unit system,

$$E = g_m \Delta w = g_m \frac{\Delta e}{P}, \quad [4]$$

where g_m is conductance in mole units ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and Δw is the leaf-to-air water vapor mole fraction gradient derived from the leaf-to-air vapor pressure difference (Δe) and barometric pressure (P). The mole fraction gradient is dimensionless, and Δe and P are in Pascals (Pa), or, more conveniently, in kPa.

When leaf and air temperatures are the same, the relationship between conductance in mole units and conductance in velocity units can be derived by equating Eqs. [2] and [4], recognizing that $\Delta e = \Delta\rho_w RT$, and rearranging to give

$$g_m = \frac{P}{RT} g_v = \rho g_v \quad (T_L = T) \quad [5]$$

Thus, mole conductance ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) is simply the mole density of air ($\text{mol}\cdot\text{m}^{-3}$) times conductance in velocity units ($\text{m}\cdot\text{s}^{-1}$) (Farquhar et al., 1978).

A sample conversion from velocity to mole units will be useful. At 30°C and a barometric pressure of $101,300 \text{ Pa}$, $\rho = 101,300 \text{ Pa} / (8.314 \text{ m}^3 \text{ Pa}\cdot\text{mol}^{-1}\cdot\text{K}^{-1} \cdot 303\text{K}) = 40.2 \text{ mol}\cdot\text{m}^{-3}$. A conductance of $1 \text{ cm}\cdot\text{s}^{-1}$ is equivalent to $0.01 \text{ m}\cdot\text{s}^{-1}$, so $40.2 \text{ mol}\cdot\text{m}^{-3} \times 0.01 \text{ m}\cdot\text{s}^{-1} = 0.40 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. A worthwhile rule-of-thumb is that $g_m \approx 40 g_v$, with g_v in $\text{m}\cdot\text{s}^{-1}$. This simple relationship is accurate to within $\pm 10\%$ from 0 to 50°C .

The pressure used to perform the conversion is the local barometric pressure, not the barometric pressure reported by the National Weather Service, because the latter value is corrected to sea level. Barometric pressure is a strong function of elevation, so it should be measured locally or it can be estimated for a standard atmosphere from $P\{\text{Pa}\} = 101,300 - (10 \text{ Pa}\cdot\text{m}^{-1}) \times \text{elevation}\{\text{m}\}$.

Under nonisothermal conditions, the relationship between mole units and velocity units is more complex. This complexity can be seen by substituting the ideal gas law into Eq. [4] and factoring out RT_L/F giving

$$E = g_m \frac{RT_L}{P} (\rho_{wL} - \frac{T}{T_L} \rho_w). \quad [6]$$

The coefficient multiplying the expression in brackets is formally equivalent to g_v in Eq. [5]; however, the gradient is different from that given in Eq. [2]. Therefore, in general, mole conductance units and velocity conductance units are not simply proportional.

A correction factor that holds under nonisothermal conditions can be derived by setting Eq. [2] equal to Eq. [6], defining $\Delta T = T_L - T$, $\Delta\rho_w = \rho_{wL} - \rho_w$, and rearranging to obtain

$$g_m = g_v \frac{P}{RT_L (1 + \frac{\rho_w}{\Delta\rho_w} \frac{\Delta T}{T_L})}, \quad (\Delta\rho_w > 0) \quad [7a]$$

or

$$g_m \approx g_v \frac{P}{RT_L} \quad [7b]$$

Using leaf temperature instead of air or average temperature partially compensates for the difference in gradient definitions under nonisothermal conditions. This result can be seen by noting that if ΔT is positive ($T_L > T$), then the correction factor in equation 7b is > 1 ; so, the effective temperature that should be used in the unit conversion is even higher than the leaf temperature. Thus, any temperature below T_L , such as air or average temperature, would be worse than T_L . A similar argument holds when ΔT is negative. The error in using equation 7b is $< 3\%$ when RH is $< 80\%$, and negligible at $< 50\%$ RH.

It can be shown from thermodynamic considerations and the kinetic theory of gases that pressure (or mole fraction) is the appropriate driving force for diffusion. Therefore, no corrections are required when mole units are converted to velocity units because the correct gradient was used from the beginning. In that case, simply use average temperature. The mole unit system is the more general of the two, and is preferred.

A third unit system variant is used by micrometeorologists. They express transpiration in terms of a vapor pressure gradient multiplied by a collection of "constants" including resistance in units of velocity $^{-1}$ (e.g., Jackson et al., 1981). This approach is equivalent to the mole unit system since it is based upon vapor pressure, not vapor density, and it can be reduced to $E = \rho g_v \Delta w = g_m \Delta w$.

Conductance in mole units depends less on temperature and pressure than does conductance in velocity units (Cowan, 1977; Farquhar, 1978). This is true because the diffusivity of water vapor in air depends strongly on temperature and pressure. Equation 3 shows that g_v is proportional to the diffusion coefficient for water vapor, and the diffusion coefficient is proportional to $T^{1.8} P^{-1}$ (e.g. Gale, 1972; Hall, 1982). Thus, multiplying g_v by $P(RT)^{-1}$ removes the pressure dependence and greatly reduces the temperature dependence inherent in g_v . As a result, conductance in mole units depends less on environmental conditions than does conductance in velocity units.

These considerations have some practical consequences. a) Use mole units if possible. b) Report temperature and pressure along with conductance if measurements are made at widely differing temperatures or elevations and conventional units are used (Parkinson, 1985b). This practice will facilitate later comparisons. c) Use leaf temperature when converting velocity units to mole units. d) Use average temperature when converting mole units to velocity; or use average temperature all the time, and errors will be small, except at high humidity ($> 70\%$).

STOMATAL RESPONSE TO A VENTILATED CUVETTE

Stomata may close when leaves are placed into a ventilated cuvette. Recently, Idso (1987) suggested that stomatal closure may be a general problem leading to discrepancies between results from porometry and those derived from infrared thermometry. He and co-workers went on to present a way to correct porometer data using a crop water stress index based upon "non-water stressed base-

lines" and energy balance considerations (Idso and Allen, 1988; Idso, et al., 1987).

However, stomatal closure is not always a problem. Other authors have found good agreement between conductances or transpiration rates measured with porometers and those computed from gravimetric measurements of plant water loss (Day, 1977; Tan and Black, 1978; Watts, 1977). Landsberg et al. (1975) and Paw U and Daughtry (1984) also found reasonably good agreement between porometer-derived conductances and conductances computed by energy balance. In addition, Day (1977) showed that stomatal conductances of several field crops were stable for up to 2 min in a ventilated flow-through porometer with high boundary layer conductance ($0.05 \text{ m} \cdot \text{s}^{-1}$).

It is likely that differences in air saturation deficit, plant water status, the frequency and intensity of natural wind, light intensity, and plant species will all influence the stability of leaf conductance in a porometer cuvette. Therefore, it is not surprising that stomatal closure might be a problem in one circumstance and not another. Neither the extent nor the cause of stomatal closure is fully understood, so porometer users should be aware of this possible artifact. More work is required in this area of research.

There are several ways to detect stomatal closure while making conductance measurements. First, it is important to recognize that stomatal closure can occur in a porometer and to watch for it. In a null-balance porometer, such as the LI-1600, view relative humidity, not conductance, while the instrument seeks the humidity set-point. When the instrument is first put onto a leaf, two variable phenomena may occur simultaneously. First, the instrument is varying the flow rate to bring the cuvette relative humidity to the humidity set-point; during this time, the conductance will appear to change, but its value is meaningless until a steady state is established. Second, the plant may be responding to conditions in the cuvette and the actual conductance may be changing. Watch the humidity until the set-point is reached, and then switch to conductance. The plant is responding to the chamber if conductance continues to change.

In the LI-6200, a series of conductances are measured over a series of short-time intervals (one or a few tens of seconds per observation). It will be immediately obvious if conductance is changing.

Changing conductance can be identified in a flow-through steady state system by a prolonged time required to achieve steady state with respect to water vapor (or CO_2). The system time constant with a constant transpiration input can be estimated from chamber volume (m^3) divided by volumetric flow rate ($\text{m}^3 \cdot \text{s}^{-1}$), or from chamber volume $\times$ air density (P/R/T) divided by mole flow rate. The chamber humidity will normally reach 95% of its steady state value after three time constants. It will take longer than this to achieve a steady state if conductance is changing. Water sorption in the system complicates this analysis by causing a larger time constant than the actual chamber volume would indicate. However, an apparent chamber volume that includes this effect can be measured in preliminary experiments (Parkinson et al., 1980) and used in the above calculation.

Several approaches present themselves as possible ways to minimize conductance changes. First, measurements should be made as quickly as possible, before substantial changes in stomatal conductance have time to occur. Stomata may be stable for minutes in some cases (Day, 1977) but start changing almost immediately in others, so there is no general guideline for how quick is quickly enough. The minimum time will be determined by the response time of the instrument, so measurement after a standard time interval may be helpful. However, such a procedure might lead to biases across some treatments.

Consideration of possible causes of stomatal closure leads to two other approaches. Idso et al. (1987) and Idso and Allen (1988) suggested that stomata close when the normally moist boundary layer air that is present in the field is swept away and replaced in the cuvette by relatively dry ambient air. This would lead to an increased leaf water loss rate, a negative water balance in the epidermis, and stomatal closure. A similar mechanism was proposed earlier by Grace et al. (1975). They showed that increasing wind

speeds led to a decline in stomatal conductance in Sitka spruce, as did an increase in air saturation deficit. Bunce (1985) followed up their observations with several broad-leaved species and found that stomatal conductance depended upon the leaf surface VPD whether it was determined by manipulations of wind speed or bulk air vapor pressure. Leaf surface VPD [or relative humidity (Ball et al., 1987)] appears to be the factor controlling stomatal opening, not bulk air VPD (Ball et al., 1987; Bunce, 1985; Grantz and Meinzer, 1989). Proper consideration of leaf surface vapor pressure as well as covariation of light, temperature, and VPD in nature, accounts for much of the apparent discrepancy between porometry and baseline analysis (Grantz and Meinzer, 1989; Monteith, 1989) described by Idso (1987) and co-workers (Idso and Allen, 1988; Idso et al., 1987).

These observations suggest that either cuvette fan speed might be reduced or chamber humidity increased or both when stomatal closure is a problem. For example, in the 1-liter chamber of the LI-6200, reducing the fan voltage from 10 to 5 V caused the boundary layer conductance to decrease from $1.3 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ to $0.7 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Boundary layer conductance changes were smaller in the 250-ml chamber over the same voltage range. Applying this idea, J.M. Norman (personal communication) found that reducing the fan speed in the 250-ml chamber did reduce stomatal closure in sensitive prairie grasses.

Traditionally, porometer designers have attempted to maximize boundary layer conductance so that it presents as small a limitation as possible (Bail, 1987; Beardsell et al., 1972; Day, 1977; Parkinson, et al., 1980; Schulze et al., 1982). However, that strategy may have to be revised when measuring very sensitive stomata. Of course, if the boundary layer conductance is decreased in a cuvette, then it becomes increasingly important that it be accurately measured. This can be done by the moist filter paper method or by energy balance (Op Cit; Parkinson, 1985a).

Depending on the system, chamber operating humidity can be increased by changing the humidity set point or the system flow rate so that chamber humidity is increased sufficiently to limit leaf transpiration to roughly field levels. If this suggestion is followed, care should be taken to allow time for the cuvette to re-equilibrate to the new humidity to minimize water sorption errors.

Effects of transpiration-induced stomatal closure on gas exchange data can be subtle and serious. Sharkey (1984) found that CO_2 response curves measured under high transpiration demands led to an apparent reduction of maximum assimilation rates in several species. We have observed a similar phenomenon in greenhouse-grown vegetative soybean (D.K.M., J.T. Ball, and J.M. Welles, unpublished data). However, the same sorts of curves would be generated if for some reason the internal CO_2 concentration (C_i) was overestimated in the presence of high transpiration rates. In that case, maximum assimilation rates would not be too low, C_i would just be too high, so the actual C_i would not be high enough to achieve maximum assimilation rates in the high transpiration treatments.

Recently, Terashima et al. (1988) showed that stomata do not close uniformly across leaves of *Helianthus annuus* or *Vicia faba* when leaves are treated with abscisic acid, and that irregular stomatal closure leads to serious overestimates of internal CO_2 concentration. Similar nonuniformity has been observed directly in *V. faba* in response to low atmospheric humidity (Kappen et al., 1987); thus, we may expect to find errors in calculating C_i under those conditions. Such errors are hard to detect and they can lead to serious misinterpretations. Thus, humidity-induced stomatal closure cannot only cause underestimates of stomatal conductance, but also erroneous CO_2 response curves and incorrect conclusions about treatment effects on the photosynthesis apparatus.

ESTIMATION OF IN SITU TRANSPIRATION RATE

It is tempting to use the transpiration rate measured in a porometer to estimate transpiration rate in situ. Don't do it. At best, leaf temperature, air temperature, and boundary layer conductance will all have different values in the porometer than in the field. At worst, stomatal conductance and VPD may be different as well. If one assumes that the measured stomatal conductance is correct, then the field transpiration rate can be computed from in situ values for air

and leaf temperatures, relative humidity, and boundary layer conductance according to Eq. [4] (Landsberg et al., 1975; Tan et al., 1978). Alternatively, transpiration or conductance can be computed from energy balance (Kanemasu et al., 1969; Landsberg et al., 1975).

It is necessary to compute total leaf conductance, g_L (called g_m in Eq. [4]), before Eq. [4] can be applied. Both stomatal conductance and boundary layer conductance must be known for each side of the leaf and then combined to give total leaf conductance. These calculations are straightforward when appropriate data are available (e.g., Ball, 1987; Nobel, 1984); however, many instruments measure conductance on both sides of a leaf simultaneously, so single-sided conductance values are not available. In addition, some method must be used to estimate the boundary layer conductance under field conditions. This second consideration will be addressed first.

Computing the boundary layer conductance is a matter of considerable complexity (e.g., Finnigan and Raupach, 1987; Gates, 1980; Grace et al., 1980; Monteith, 1973), but several formulas have been put forward to estimate its value under various conditions. In the simplest case, where wind speeds are low or moderate and air flow is laminar, the formulas have the form $g_b = C(v/d)^{1/2}$ for a one-sided boundary layer conductance, where C is a coefficient that varies with leaf shape, fluttering, air stream angle of attack, and turbulence intensity (Finnigan and Raupach, 1987; Nobel, 1984); d is the average linear leaf dimension (m) in the direction of the wind (Grace et al., 1980), and v is the wind speed ($m \cdot s^{-1}$). The value of C (g_b in $m \cdot s^{-1}$) calculated from Finnigan and Raupach (1987) is ≈ 0.0069 ($\pm 50\%$); from Nobel (1984) the value is ≈ 0.0062 , and Norman (personal communication) recommends 0.0056. The following expressions are useful approximations for boundary layer conductance.

$$g_b \approx 0.006 (v/d)^{1/2} \pm 50\% \{m \cdot s^{-1}\} \quad [8]$$

$$\approx 0.24 (v/d)^{1/2} \{mol \cdot m^{-2} \cdot s^{-1}\}$$

The average length for leaves that are not lobed is given by $d = (\sum d_i)/n$, where d_i is the length of the i th chord running from leaf edge to edge parallel to the direction of the wind, and n is the number of chords measured. For lobed leaves, see Grace et al. (1980).

Once in situ boundary layer conductances are known for each side of the leaf, they must be combined with the upper (u) and lower (l) surface stomatal conductances. If the upper and lower stomatal conductances are measured independently as, for example, with the LI-1600 or DELTA-T Automatic Porometer, Mk 3 (Delta-T Devices, Cambridge, U.K.), then the total leaf conductance (g_L) is given by

$$g_L = g^u_L + g^l_L, \quad [9]$$

where

$$\frac{1}{g^u_L} = \frac{1}{g^u_s} + \frac{1}{g^u_b}, \quad [10]$$

g^l_L is defined similarly.

Systems such as the ADC LCA, LI-6200 and many others measure water loss from both sides of a leaf simultaneously, so independent data for the two surfaces are often not available. Some knowledge of the ratio of stomatal conductances (or frequencies) on the two sides of the leaf, and an assumption about boundary layer conductance on the upper and lower leaf surfaces is necessary to complete the calculation. Boundary layer conductance may be different on the two leaf surfaces because of leaf angle, shape, venation, etc., but the uncertainty in computing it justifies the assumption that it is the same on both sides of the leaf. With this assumption and the definitions $K = g^l_s/g^u_s$, and $g_s = g^u_s + g^l_s$, Eqs. [9] and [10] can be combined to give

$$g_L = \frac{1}{\frac{1}{g_s} + \frac{1}{g_b}} + \frac{K}{\frac{1}{g_s} + \frac{K}{g_b}} \quad [11]$$

Usually, some estimate of K will be available because it is required

for computation of g_s from a two-sided measurement in the porometer. Fortunately, the value of K need not be known with great accuracy, and the impact of an error in K decreases as g_s decreases. For example, if g_b is taken as $1 \text{ mol} \cdot m^{-2} \cdot s^{-1}$, and the true value of $K = 2$ is estimated as $K_{\text{estimate}} = 4$ (or 0.25), then the estimated value of g_s will be in error by 3.6% when the true value is $0.3 \text{ mol} \cdot m^{-2} \cdot s^{-1}$, and by 10.3% when the true value is $1.5 \text{ mol} \cdot m^{-2} \cdot s^{-1}$. Thus, g_s is not very sensitive to even serious errors in K . Equation 11 is symmetrical with respect to the definition of K ; it does not matter whether K is defined as upper/lower or lower/upper.

The in situ transpiration rate can now be computed from the local relative humidity, air temperature, and wind and speed in the leaf vicinity and from the leaf temperature using Eqs. [4], [8], and [9] and [10], or [11]. Tables or equations for determining saturation vapor pressure from temperature are readily available (Buck, 1981; List, 1984; Lowe, 1977).

CONCLUSIONS

Porometry can yield accurate estimates of stomatal conductance in many conditions; however, there are limitations that should be recognized. For example, relative humidity measurements with capacitive sensors will be difficult at high humidities ($>80\%$ RH), and those problems are magnified by the high conductance sensitivity to humidity measurement errors when humidity is elevated. This situation is ameliorated somewhat when leaf temperature is above air temperature, as shown in Figs 5, 6, and 7.

Rapid stomatal closure in the porometer cuvette is another problem that can limit porometer accuracy in certain cases. There is substantial variation in sensitivity to leaf surface humidity among plants (Bunce, 1985; El-Sharkawy et al., 1985); and the extent to which 3 porometer alters the leaf surface humidity depends on the operating conditions in the cuvette and on the conditions existing in nature before the measurement is made. Watch for stomatal closure. If it is a problem: a) make rapid measurements (60s or less), b) reduce boundary layer conductance by slowing the fan speed, or c) consider operating the porometer at a slightly elevated humidity, e.g., 5% to 15% RH above ambient. The third suggestion should only be applied in steady state; otherwise water sorption will cause errors.

The responsiveness of all sensors should be checked prior to using the porometer. The leaf temperature thermocouple is most important in this regard because a broken thermocouple is easily overlooked. A finger gently placed on the thermocouple will quickly show whether or not the sensor is working.

The importance of humidity sensor calibration cannot be over-emphasized. A rough check of humidity sensor calibration can be accomplished by measuring the RH of dry air (0% to 2% RH depending on the drying agent) and the RH of your breath ($\approx 96\%$ RH). Better still, check the humidity sensor against a known source if equipment is available. Beyond daily precautions, all of the sensors, and particularly the humidity sensor, *must* be thoroughly recalibrated at least once every season, or more often as the results of these simple checks dictate.

Many porometers use a desiccant to provide dry air. The desiccant must be kept fresh to obtain accurate results.

Several unit systems are widely used for expressing porometer data. Mole units are recommended because they are less sensitive to temperature and pressure than velocity units, and because they are based on a water vapor mole fraction gradient that is thermodynamically correct. It will facilitate later comparisons if temperature and pressure are reported when conductance data are expressed in velocity units (Parkinson, 1985b). Use leaf temperature, not air or average temperature, when converting velocity units to mole units.

The transpiration rate measured in a porometer generally will not be the same as transpiration in the field. Field transpiration rates should be computed from in situ values of air temperature, leaf temperature, wind speed and bulk air relative humidity, along with the stomatal conductance measured in the porometer; or it can be estimated from energy balance considerations.

(Note added in proof: Two new porometers have appeared since this paper was written. Delta-T Devices (Cambridge, U.K.) has

introduced the Porocorder, a porometer that uses the same measurement principle as the Delta-T Mk III, but now provides automatic reference to a calibration curve, among other features. Analytical

Development Corp. (Hoddeson, Herts, U.K.) has introduced the LCA-3, a CO₂ and water vapor porometer in which chamber humidity and flow rate can be independently controlled, within limits.]

Appendix Symbols and units.

C	Boundary layer coefficient ($\text{m}\cdot\text{s}^{-1/2}$)
D	Diffusion coefficient of water vapor in air ($2.5 \times 10^{-5} \text{ m}^2\cdot\text{s}^{-1}$ at 20C)
d	Average linear leaf dimension in direction of wind (m)
E	Transpiration rate ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
e	Vapor pressure of chamber air (Pa or kPa)
e _i	Vapor pressure of chamber inlet air (Pa or kPa)
e*(T)	Saturation vapor pressure at temperature T (Pa or kPa)
Δe	Vapor pressure difference between leaf and air (Pa or kPa) = e*(T _L) - e
de/dt	Chamber air vapor pressure rate of change ($\text{Pa}\cdot\text{s}^{-1}$ or $\text{kPa}\cdot\text{s}^{-1}$)
ξ	Dummy variable representing any variable in the conductance equations
g _b	Boundary layer conductance ($\text{m}\cdot\text{s}^{-1}$ or $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
g _b ^l , g _b ^u	Boundary layer conductance of lower (l) or upper (u) leaf surface
g _s	Stomatal conductance ($\text{m}\cdot\text{s}^{-1}$ or $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
g _s ^l , g _s ^u	Stomatal conductance of lower (l) or upper (u) leaf surface.
g _L	Total leaf conductance ($\text{m}\cdot\text{s}^{-1}$ or $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
g _L ^l , g _L ^u	Total conductance of lower (l) or upper (u) leaf surface
g _m	Mole conductance ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
g _v	Conventional conductance in velocity units ($\text{m}\cdot\text{s}^{-1}$)
Δg	Absolute error in conductance
h	Fractional chamber humidity (= RH/100%, dimensionless)
h _e	Expected fractional humidity of chamber inlet air
h _i	Fractional humidity of chamber inlet air
Δh	Error in chamber humidity measurement
Δh _i	Error in inlet air humidity measurement
K _{abs}	Water sorption correction parameter in LI-6200
n	Number of chords used to compute average leaf dimension, L
ρ	Air density [= P(RT) ⁻¹ , $\text{mol}\cdot\text{m}^{-3}$]
ρ _w	Water vapor density of chamber air ($\text{mol}\cdot\text{m}^{-3}$)
ρ _{wL}	Water vapor density inside a leaf ($\text{mol}\cdot\text{m}^{-3}$)
Δρ _w	Water vapor density difference between leaf and air ($\text{mol}\cdot\text{m}^{-3}$)
P	Local barometric pressure (Pa or kPa)
r	Ratio, e*(T _L)/e*(T) (dimensionless)
R	Gas constant (= 8.314 Pa m ³ ·mol ⁻¹ ·K ⁻¹)
RH	Relative humidity (%)
T	Chamber air temperature (Kelvin, K)
ΔT	Air temperature measurement error (K)
T _L	Leaf temperature (K)
ΔT _L	Leaf temperature measurement error (K)
u	Air flow rate ($\text{mol}\cdot\text{s}^{-1}$)
v	Wind speed ($\text{m}\cdot\text{s}^{-1}$)
V	Chamber volume (m ³)
VPD	Leaf-to-air water vapor pressure difference (= Δe, Pa or kPa)
λ	Latent heat of water vaporization (= 43.7 kJ·mol ⁻¹ at 30C)

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