
8

Measurement of transpiration and leaf conductance

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8.1 INTRODUCTION

Measurements of leaf transpiration and calculations of leaf conductance to water vapor are important in almost all investigations of plant water relations. Transpiration is a primary determinant of leaf energy balance (Chapter 7) and plant water status (Chapter 9). Together with the exchange of CO₂ it determines the water use efficiency. The close linkage between CO₂ uptake and H₂O via the stomatal pore has allowed for separation of stomatal and biochemical limitations to photosynthesis through calculation of intercellular CO₂ concentrations. In this chapter we will cover the principles and instruments necessary for measurement of leaf transpiration and the calculation of leaf conductances to water vapor exchange. We will also consider the methodology and problems involved in determining whole-plant and canopy transpiration rates. Emphasis is placed on methods and equipment that have as their primary purpose, the direct measurement of transpiration rates or leaf conductance to water vapor loss. It should be noted that in many research problems, knowledge of both CO₂ and H₂O exchange are required. In the

past, porometers that measure only leaf conductance to water vapor have sometimes been used to infer more general environmental response of gas exchange including CO₂ uptake. While a general correlation is expected, direct measurements of CO₂ exchange, which are much more feasible than even a few years ago, are clearly more appropriate. Field equipment designed for simultaneous measurements is covered primarily in Chapter 11. In this chapter we will, however, cover the water vapor sensors and the theory and procedures necessary to measure transpiration and calculate stomatal conductances in these systems.

8.2 LEAF TRANSPIRATION RATE

Measurements of transpiration and the calculation of water vapor conductances of single leaves are nearly always based on the measurement of vapor added by transpiration into the air inside a chamber enclosing the leaf or a leaf surface (Jarvis and Catsky, 1971). In an 'open' system, a flow of air passes through the chamber and the leaf transpiration rate is calculated from the difference in water

vapor content of the air entering and leaving the chamber, the flow rate and the leaf area. A typical 'closed' system would have the leaf enclosed for a short period of time in a chamber along with a humidity sensor so that the rate of transpiration is a function of the rate of increase of humidity in the chamber. Closed systems, while useful for photosynthesis measurements (see Chapter 11), have limited applicability for determination of transpiration rates because the increasing air humidity causes a reduction in the vapor pressure gradient from the leaf to the air and, consequently, a reduction in the transpiration rate. This, combined with problems of water vapor adsorption to the chamber which will be discussed below, render them much less useful and reliable than open systems even though they require less instrumentation.

In an open system (Fig. 8.1), the leaf transpiration rate is equal to the additional amount of water vapor leaving the chamber above that entering. The water vapor added by the leaf via transpiration (E , $\text{mol m}^{-2} \text{s}^{-1}$) is given by:

$$EL = u_o w_o - u_e w_e \quad [\text{mol s}^{-1}] \quad (8.1)$$

where w_e and w_o (mol mol^{-1}) are the mole fractions of water vapor (mol of water vapor per total mol of all gases) in the entering and outgoing air streams respectively, L (m^2) is the leaf area and u_e and u_o (mol s^{-1}) are the total molar flow rates (air plus water vapor) entering and leaving the chamber, respectively. If the flow meter is calibrated in volumetric or mass units, molar flow rate is obtained by applying the ideal gas law.

Using Dalton's law of partial pressures, which states that the mole fraction of a gas in a mixture is equal to its partial pressure, w_o and w_e can be calculated from measurements of vapor pressure (v_w , Pa) or relative humidity (R , %). If vapor pressure is measured then:

$$w = \frac{v_w}{P} \quad [\text{Pa Pa}^{-1}] \quad (8.2)$$

where P is the total air pressure at the humidity sensor. If relative humidity is measured then:

$$w = R \left(\frac{v_{w, \text{sat}}}{P \times 100} \right) \quad [\text{Pa Pa}^{-1}] \quad (8.3)$$

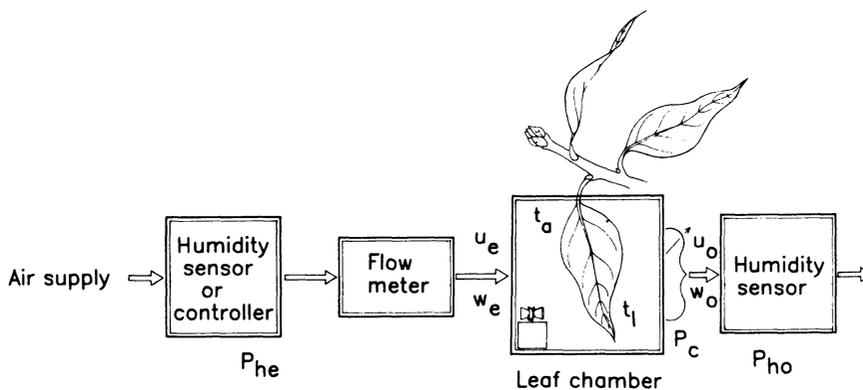


Fig. 8.1 Functional block diagram of an 'open' system for measurement of transpiration. The flow rate of air in mol s^{-1} into (u_e) and out of (u_o) the chamber, including the leaks and the mole fractions of water vapor entering (w_e) and exiting (w_o) the chamber must be known. Pressures must be known at the humidity sensors (P_{he} , P_{ho}) and in the chamber (P_c). Leaf (t_l) and air (t_a) temperatures in the chamber must be measured.

where $v_{w,\text{sat}}$ is the saturation water vapor pressure at the temperature of the humidity sensor. Air pressure can be determined by adding the pressure measured at the humidity sensors either with simple water manometers or electronic differential pressure sensors to the atmospheric pressure measured with a barometer (see Chapter 4). Alternatively, an absolute pressure transducer can be used. If the additional pressure in the system above atmospheric pressure does not exceed 0.5 kPa or so, it can be ignored, whereas atmospheric pressure varies considerably with elevation and weather.

Special consideration must be given to the determination of gas flow rates. Because of conservation of mass, the total outgoing flow from the chamber must exceed the entering flow by the amount of water vapor added by the leaf. Measurement of the flow downstream of the chamber is impractical because it is usually not possible to seal the chamber completely. Therefore the flow meter is mounted upstream of the chamber. Leaks in the chamber or after it are then usually of little consequence provided that the chamber atmosphere is well mixed so that the humidity measurement is a true sample of the air leaving the chamber by all routes, including the leaks. The total flow out of the chamber is then calculated from the entering flow plus the additional flow of water vapor. Since the difference in the flow is equal to the evaporation from the leaf, Equation 8.1 can be rewritten as

$$u_o - u_e = u_o w_o - u_e w_e \quad [\text{mol s}^{-1}] \quad (8.4)$$

and therefore with rearrangement,

$$u_o = u_e \left(\frac{1-w_e}{1-w_o} \right) \quad [\text{mol s}^{-1}] \quad (8.5)$$

Equation 8.5 can be substituted into Equation 8.1, with rearrangement, to yield the correct relationship for calculation of the transpiration rate of a leaf:

$$E = \frac{u_e(w_o - w_e)}{L(1-w_o)} \quad [\text{mol m}^{-2} \text{ s}^{-1}] \quad (8.6)$$

Transpiration rates should be presented using SI conventions of units of $\text{mmol m}^{-2} \text{ s}^{-1}$ or by conversion to mass units of $\text{mg m}^{-2} \text{ s}^{-1}$. Because we are frequently interested in comparing fluxes of water vapor and CO_2 , molar units are generally preferable.

Leaves can have stomata on both sides and therefore transpire from either one or both surfaces. With broad leaves, however, the convention is to take the area of only one surface. With needles, stems or other surfaces there is no standard procedure and either the projected surface area, one half of the total area or the total surface area have been used. However, as long as the convention is clearly stated and followed consistently, the result will be comparable with other published work.

8.3 LEAF CONDUCTANCE TO WATER VAPOR

Transpiration rates measured in chambers are not useful parameters in themselves since they depend on properties of the particular chamber environment as well as those of the plant. It is usually very difficult to match the chamber environment to that of a leaf outside of the chamber closely enough so that the measured transpiration rates will be representative of the outside leaves. Thus a conductance of the leaf to water vapor loss is derived from the transpiration rate. Conductances are usually presented rather than their inverse, a resistance, since conductances are proportional to the flux and they express the regulatory control exerted by the stomata on transpiration rates. If transpiration rates representative of leaves in their natural environment are needed then it is necessary to determine leaf temperatures as well as the vapor pressure of the atmosphere and then

recalculate a transpiration rate using the stomatal conductance determined in the chamber and a boundary layer conductance (see Section 8.3.3). Since stomata respond to the microenvironmental conditions, an important condition for the recalculation of natural transpiration rates is that the chamber conditions be sufficiently close to natural conditions that the stomatal conductances do not change when the leaf is enclosed or that the measurement be completed before the stomata have time to respond.

Conductance to water vapor loss (g_w) is derived from Ficks law of diffusion (see Nobel, 1984) and can be expressed in its simplest form as the proportionality between the rate of transpiration (E) and the driving force for evaporation, the gradient in water vapor from the intercellular spaces in the leaf to the atmosphere (ΔW)

$$g_w = \frac{E}{\Delta W} \quad (8.7)$$

If ΔW is expressed as a mole fraction gradient (mol mol^{-1}) and E is in molar units ($\text{mol m}^{-2} \text{s}^{-1}$) then the units of g_w are $\text{mol m}^{-2} \text{s}^{-1}$. Formerly, ΔW was expressed as a concentration gradient (g m^{-2}) and E in mass units ($\text{g m}^{-2} \text{s}^{-1}$), giving g_w units of m s^{-1} . The relative merits of expressing g_w in molar units are discussed in Section 8.3.1.

The water vapor gradient, ΔW , can be determined from the difference in vapor pressure in the chamber and the saturation vapor pressure in the intercellular air spaces. In a well-stirred chamber, the mole fraction of water vapor in the chamber (w_a) is equal to that in the airstream exiting the chamber (w_o). If the chamber is not well stirred by a fan then it will be some average of the mole fractions in the ingoing and exiting air streams. Jarvis and Catsky (1971) discuss the various assumptions regarding mixing in the chamber and show that if the chamber is not mixed and if the change across the chamber is less than one-half of the entering mole fraction, then a linear average [$w_a = (w_o + w_e)/2$] gives

a reasonable estimate. Since the air near the cell walls is assumed to be saturated with water vapor, the mole fraction in the intercellular spaces (w_i) is derived from the saturation vapor pressure at the leaf temperature divided by the total pressure (see Appendix Table A7). Thus,

$$\Delta W = w_i - w_o \quad [\text{mol mol}^{-1}] \quad (8.8)$$

Recent experiments suggest that the assumption of water vapor saturation in the intercellular spaces near the cell walls is essentially valid for well-watered plants (Sharkey *et al.*, 1982; Mott and O'Leary, 1984). A water potential of -2 MPa at a leaf temperature of 25°C equilibrates with a relative humidity of 98.5% in the intercellular spaces and therefore results in only a very small change in w_i from that at 0 MPa. Water potential effects can become significant at a combination of high relative humidities and low water potentials.

Accurate leaf temperature measurements are critical since small errors can have more than proportional effects on the estimation of

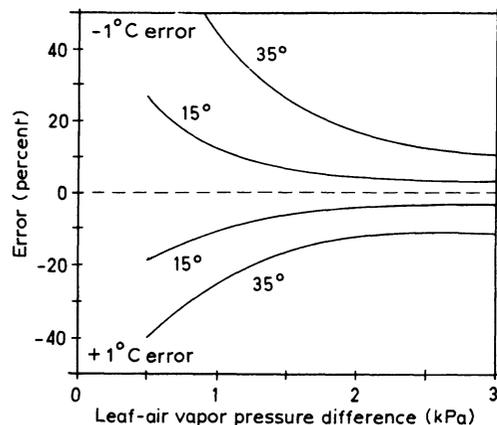


Fig. 8.2 The effect of a 1°C error in leaf temperature on the calculated conductance from measurements of transpiration in a leaf chamber. Errors are shown as a function of the true leaf-air vapor pressure difference at 15°C and 35°C . The upper and lower lines are for a -1°C and $+1^\circ\text{C}$ error respectively.

ΔW , particularly if the measurements are performed at high humidities where ΔW is small. The problems that are frequently encountered are that temperature is not uniform across a leaf and is not sampled adequately, or that there is insufficient thermal contact between the sensor (usually a thermocouple) and the leaf. Fig. 8.2 shows the error in g_w resulting from a 1°C error in leaf temperature at different temperatures and vapor pressure deficits. Ideally, leaf temperatures should be measured to an accuracy of $\pm 0.1^\circ\text{C}$ but this is rarely achieved. Precautions for making accurate leaf temperature measurements are discussed in Chapter 7.

8.3.1 Conductance units

While conductances based on concentration differences and having units of mm s^{-1} are commonly seen, particularly in the older literature, Cowan (1977) derived an alternative formulation that has several distinct advantages and is receiving increasing use. If we apply Ficks law, expressing the concentration gradient as a finite difference and ignoring additional corrections for the time being (see Section 8.3.2), then:

$$E = D_{\text{wa}} \frac{\Delta\rho}{\Delta X} \quad (8.9)$$

where $\Delta\rho$ is the water vapor density gradient from the leaf to the air, ΔX is the effective length of the diffusion path (m) and D_{wa} is the binary diffusion coefficient of water vapor in air ($\text{m}^2 \text{s}^{-1}$). It follows that

$$g_w = \frac{D_{\text{wa}}}{\Delta X} \quad (8.10)$$

According to Fuller *et al.* (1966) D_{wa} is dependent on temperature (T) and pressure (P) as follows

$$D_{\text{wa}} = D_{\text{wa}}^0 \left(\frac{T}{T_0} \right)^{1.8} \left(\frac{P_0}{P} \right) \quad (8.11)$$

where D_{wa}^0 equals the diffusion coefficient at standard temperature (T_0 ; 273°C) and pressure (P_0 ; 101.3 kPa). Because of the temperature and pressure dependence of D_{wa} and also of water vapor concentration, conductance based on concentration gradients (g m^{-3}) are dependent on temperature and pressure. Thus, even if vapor pressure gradients and stomatal apertures and densities are identical for two leaves, the conductances will differ if the measurements are made at different pressures or temperatures. For example, it can be shown by substituting Equation 8.11 into Equation 8.9, and adjusting the water vapor concentrations using the gas law, that a temperature increase from 20 to 30°C will increase the calculated value of g by 6.3% . A change from sea level to 1000 m elevation will result in a 10% higher calculated value of g_w even with no change in stomatal aperture.

Mole fractions, however, are independent of temperature and pressure. By using the gas law to convert a concentration gradient to a mole fraction gradient, it can be shown that g_w is proportional to $T^{1.8}$ if concentrations are used and to $T^{0.8}$ if mole fractions are used (see Hall, 1982; Nobel, 1984). Consequently, the change from 20 to 30°C causes only a 2.8% increase in g calculated from the mole fraction gradient. Moreover, g_w expressed in molar units is independent of pressure. Molar units are easily used since E and g have the same dimension. Thus, ΔW expressed as a dimensionless mole fraction multiplied by g_w in molar units results in E having molar units. We recommend that molar units be used whenever possible. Conversion of conductances in units of cm s^{-1} to molar units is easily done, assuming isothermal conditions, if pressure and temperature are known since:

$$g_w(\text{mol m}^{-2} \text{s}^{-1}) =$$

$$g_w(\text{cm s}^{-1}) 0.446 \left[\frac{273}{(T+273)} \right] \left[\frac{P}{101.3} \right] \quad (8.12)$$

where temperature is in °C and pressure is in kPa. Appendix Table A9 gives conversion factors for a range of temperatures and pressures.

If conditions are not isothermal then it can be shown that the error is minimized by using leaf temperature (D. McDermitt, personal communication). However, even for a relatively large leaf–air temperature difference of 5°C within a chamber the error is less than 1–2%.

8.3.2 Calculation of total conductances to water vapor

Equation 8.7 is not strictly true because the evaporation rate through the stomatal pore is driven not only by diffusion but also by a small mass flow. When water evaporates in the intercellular spaces it displaces air causing a small mass flow through the stomatal pore. This flow carries with it a small amount of water vapor that must be added into the strictly diffusional movement of water vapor. In addition, the diffusional movements of water vapor, air and CO₂ can interact (see Jarman, 1974; von Caemmerer and Farquhar, 1981), slightly altering the diffusion of each. However, the effect of CO₂ diffusion on water vapor diffusion is negligible because of the much lower concentration of CO₂ than water vapor. But the additional transpiration occurring because of mass flow is significant and is equal to the mean water vapor mole fraction along the stomatal and boundary layer path times the evaporation rate. Thus, Equation 8.7 becomes:

$$E = g_{tw}(w_i - w_a) + E \left(\frac{w_i + w_a}{2} \right) \quad [\text{mol m}^{-2} \text{ s}^{-1}] \quad (8.13)$$

Rearranging Equation 8.13 yields:

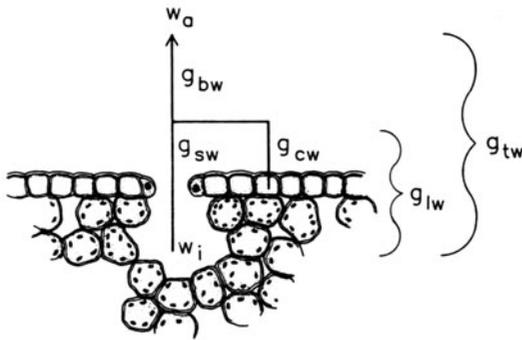
$$g_{tw} = \frac{E \{1 - [(w_i + w_a)/2]\}}{w_i - w_a} \quad [\text{mol m}^{-2} \text{ s}^{-1}] \quad (8.14)$$

The value of $(w_i + w_a)/2$, which is the mean water vapor concentration along the diffusion path from inside the leaf to the atmosphere, is typically 0.020 to 0.035 so that the correction is on the order of –2 to –3.5%. While it is small, the correction is easily made and should be done. These corrections are especially important for calculation of CO₂ conductances and intercellular CO₂ pressures (see Chapter 11).

8.3.3 Calculation of stomatal conductances

The g_{tw} calculated in Equation 8.14 is a total leaf conductance to water vapor and includes, in addition to the stomata, the pathway through the cuticle and the effect of the boundary layer. Thus, in order to calculate a stomatal conductance, the network of water loss pathways needs to be considered (Fig. 8.3). Conductances that are in parallel, such as those for two sides of a leaf or for stomata and the cuticle, are additive. However, for conductances that are in series, such as those for the stomata and boundary layer, the reciprocal of the total conductance is equal to the sum of the reciprocals of the conductances (= sum of the resistances).

Under most circumstances, the cuticular conductance, g_{cw} , can be ignored because it usually appears to be very small relative to stomatal conductance, g_{sw} , when the stomata are open. However, when the stomata are closed such as in low light or under conditions of water stress, a significant fraction of the transpiration may occur across the cuticle, leading to erroneous estimates of g_{sw} . These errors can be important when g_{sw} is used to calculate intercellular CO₂ pressures (see Chapter 11). Unfortunately, there is no readily apparent way to evaluate g_{cw} independent of the stomata. While g_{cw} can be measured for the abaxial surface of a hypostomatous leaf, there is no easy way of knowing if this value would apply to the abaxial cuticle as well. Similarly, g_{tw} measured in the dark may be close to g_{cw} but one cannot be sure that the stomata were fully closed.



Parallel:

$$g_{lw} = g_{sw} + g_{cw}$$

$$g_{sw} = g_{lw} \text{ if } g_{sw} \gg g_{cw}$$

Series:

$$\frac{1}{g_{sw}} = \frac{1}{g_{tw}} - \frac{1}{g_{bw}} \quad \text{or:}$$

$$g_{sw} = \frac{g_{tw} g_{bw}}{g_{bw} - g_{tw}}$$

Fig. 8.3 Network of conductances at the leaf surface showing the rules for simplifying complex networks to calculate the stomatal conductance to water vapor.

The boundary layer conductance, g_{bw} , is an important component in the path for water vapor loss and must be included in any analysis. In a well-stirred chamber, g_{bw} is usually much larger than g_{sw} so that the primary component in the total conductance is g_{sw} . The boundary layer conductance can be evaluated using wet filter paper replicas of the leaf (see Chapter 4) and after taking the reciprocals, subtracted to yield $1/g_{sw}$. Because of the series path through the stomata and boundary layer, the gas exchange through the two sides of a leaf should ideally be measured independently in a double-sided chamber. However, if g_{bw} is large relative to g_{sw} , then little error results by calculating an average conductance from measurements where both surfaces are enclosed within a single chamber (Jones, 1983).

8.4 INSTRUMENTATION FOR TRANSPIRATION MEASUREMENTS

In order to measure transpiration and calculate conductances, accurate determinations of vapor pressures, air flow and leaf tempera-

tures are necessary. The measurement of leaf temperatures is covered in Chapter 7 and air flow in Chapter 11. Consequently, only humidity sensors will be covered here.

There is a large variety of humidity sensors available and many types have been used with varying degrees of success in measurements of transpiration. Most humidity sensors have been developed for industrial applications of sensing humidity levels but not for flux rate measurements where accuracy and repeatability requirements are more demanding. Some other highly accurate techniques function over only narrow humidity ranges. Thus, of the many techniques available for measuring humidity, only a few are appropriate for use in measuring transpiration under field conditions. Among those developed for industrial applications are lithium chloride dew cells, Dunmore cells and carbon resistance elements. All of these provide an electrical output that is a function of relative humidity or dew point of the air but none possesses the stability and accuracy necessary for transpiration measurements. They tend to be slow, quite temperature dependent and exhibit considerable hysteresis. Psychrometric systems based on wet- and dry-bulb thermo-

couples have also been used under laboratory conditions (Slatyer and Bierhuizen, 1964), but these are not as reliable or as convenient as other sensors that are now available. Only infrared water vapor analyzers, dew-point mirrors and thin-film capacitance-type sensors are presently used in transpiration measurements.

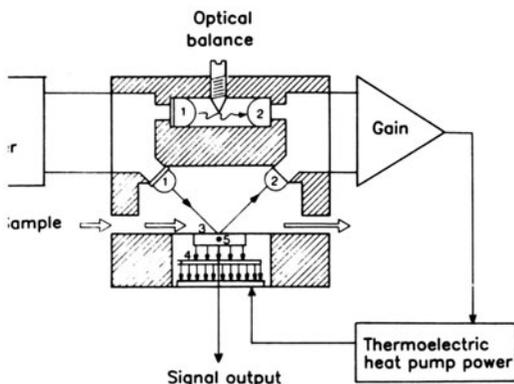
8.4.1 Infrared gas analyzers

Infrared gas analyzers are typically used in ecophysiology for measurement of CO₂ but can be made with a water vapor detector. In contrast to the CO₂-filled luft-type detector found in most CO₂ analyzers, those in water vapor analyzers are filled with ammonia, which has infrared absorption bands that overlap those of water. Infrared water vapor analyzers suitable for transpiration measurements are manufactured by Leybold-Heraeus (West Germany) and Analytical Development Co. (Great Britain). Infrared water vapor analyzers provide one of the most accurate and sensitive methods for measuring either absolute water vapor pressures or the difference in vapor pressure between two gases. The disadvantages are that they are expensive and bulky and require relatively large amounts of power. Consequently, they are best suited for transportable systems but not truly portable systems. The only analyzers specifically suited for field measurements are the Binos analyzers from Leybold-Heraeus (West Germany), which can be operated from battery power, are relatively insensitive to vibration, and are available in versions for simultaneously measuring water vapor and CO₂ pressures. Analyzers for measuring absolute water vapor pressure are suitable when transpiration rates are moderate to high. With low transpiration rates, such as those occurring in many conifers or in desert plants under water stress, differential analyzers that can be used to measure the difference in water vapor pressure of the ingoing and outgoing air steam of the

chamber may be preferred. Differential analyzers are more difficult to calibrate since it is necessary to establish known differences in water vapor concentration at several different reference concentrations. Leybold-Heraeus now manufactures an analyzer having split cells (model 452) that is capable of both differential and absolute water vapor and CO₂ pressure measurements. This model, although expensive, gives maximum flexibility and convenience by combining all gas measurements in a single instrument.

8.4.2 Dew-point mirrors

Dew-point mirrors operate by chilling a mirror with a small Peltier unit (a thermoelectric heat pump) until water vapor from the air above it condenses. The point of condensation is detected with a small light source (usually a light-emitting diode) and a photodetector (Fig. 8.4). The condensed water scatters the light so that less light reaches the photodetector than when no condensation is on the mirror. A feedback control circuit from the photodetector to the Peltier power supply controls the temperature of the mirror such that water vapor is just condensing. At this point the mirror temperature, which is measured with a thermistor or a platinum resistance thermometer, is equal to the dew-point temperature of the surrounding air. Dew point mirrors can resolve dew points of $\pm 0.1^\circ\text{C}$ with an accuracy of $\pm 0.2^\circ\text{C}$. The major limitations are the tendency for the mirror to become contaminated by aerosols, which shift the condensation point to higher temperatures, and the relatively slow response. Some systems include detection and correction circuits that eliminate the effect of optical contamination by dust, etc. However, these circuits will not correct errors due to deposited salts or organic compounds that alter the vapor pressure of the condensed water. A platinum resistance thermometer (PRT) is the preferred sensor for measuring



- 1 Light emitting diode (LED)
- 2 Photodiode
- 3 Mirror
- 4 Peltier heat pump
- 5 Platinum resistance thermometer

Fig. 8.4 Diagram showing the major components of a dew-point mirror. Adapted from literature from General Eastern.

the mirror temperature because of its accuracy and stability.

Dew-point mirror systems suitable for field use in transportable gas-exchange systems are available from H. Walz (model STR14) in West Germany and General Eastern (model Dew 10) in the United States. The Dew 10 sensor is manufactured primarily for industrial humidity control applications but has proven useful for transpiration measurements both in the laboratory and field. Both are quite compact and easily adapted for measurements in gas streams associated with leaf chambers. Both require 24 V power at a maximum of 300 mA. Both use PRT temperature sensors and for the most accurate measurements, a three- or four-wire resistance measuring circuit is required. One particular advantage is that dew-point mirrors can function at the high humidities characteristic of environments such as tropical or boreal forests where other sensors are often less reliable. But dew-point mirrors require careful maintenance if they are used to measure the dew-point differences of ingoing and outgoing air of a chamber with sufficient accuracy.

8.4.3 Thin-film capacitance sensors

These sensors consist of a thin hygroscopic polymer film separating two metal electrodes that are deposited on a thin glass chip as support. The first electrode is deposited on the glass followed by the $1\ \mu\text{m}$ thick polymer film. The second electrode is then deposited on to the film (Fig. 8.5). This second electrode is sufficiently thin (approx. $0.02\ \mu\text{m}$) that water molecules can diffuse through it and enter the pores of the film, changing the electrical capacitance of the sensor (Salasmaa and Kostamo, 1975, 1986). The change in capacitance is measured by exciting the sensor and a reference capacitor with a high-frequency AC voltage. A demodulator circuit then produces a voltage proportional to the change in capacitance (humidity). By careful adjustment of the properties of the polymer and electrodes, these sensors can be made to respond nearly linearly from 10 to 80% relative humidity. The temperature coefficient is about $0.05\% \text{ } ^\circ\text{C}^{-1}$ and the time constant is about 1 s at 25°C . It is important that they be excited at high frequencies, which was not done in some early circuits (Bingham *et al.*, 1980), since at lower frequencies the response is nonlinear and more temperature dependent. Above 80% relative humidity thin-film capacitance-type sensors typically exhibit hysteresis because additional water vapor is slowly absorbed and causes swelling of the film, resulting in an output that changes for hours. Upon returning the sensor to lower

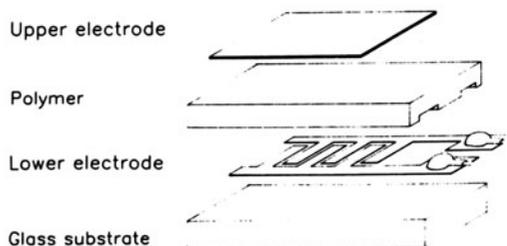


Fig. 8.5 Exploded diagram of a thin-film capacitance sensor (Vaisala Humicap).

humidities, the additional water vapor is only slowly lost. Some of the newer versions of the sensor have improved response at high humidities achieved by changing the polymer characteristics but the hysteresis has not yet been entirely eliminated. This is one of the most serious limitations to the operation of portable porometers utilizing these sensors in humid environments such as tropical forests. Thin-film sensors can be damaged by contaminants such as sulfur dioxide which oxidize the electrodes.

Thin-film capacitance sensors are inexpensive and compact, and are easily mounted within a porometer chamber. They are available from several companies. Those manufactured by Vaisala in Finland and by Coreci in France have been used as humidity sensors in transpiration measurements but others are probably suitable as well. Tables comparing the various sensors have been compiled by Schurer (1986). Thin-film capacitance sensors are probably the sensor of choice for porometers where true portability is a priority. Provided that the sensor is not exposed to

high humidity, the sensitivity is very stable. There is, however, a tendency for the offset to drift but this can be corrected for by periodically comparing the measured output to a known humidity using, for example, one of the simple dew-point columns (see Section 8.5.2). Any offset drift can then be added or subtracted from the signal to give the true humidity.

With some precautions, thin-film capacitance sensors can also function well in transportable gas-exchange apparatus. In general they are satisfactory in null-balance instruments. For differential measurements of incoming and outgoing air it is necessary to thermostat the sensors and to provide a system for conveniently checking the zero against air with a known water vapor pressure obtained, for example, from a thermostated condenser column. Thermostating can be achieved by mounting the sensors in a temperature-controlled block (Fig. 8.6). The air stream and the sensor temperature can thus be raised so that relative humidity never exceeds 60%, avoiding problems with hys-

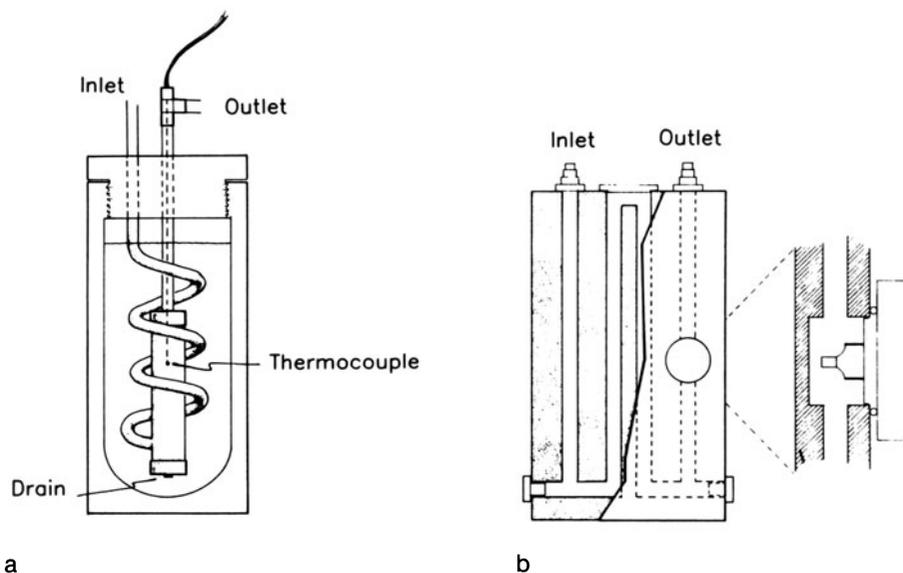


Fig. 8.6 (a) A calibration system for humidity sensors using a simple copper tubing column in an insulated flask of the type used to hold hot drinks. (b) Diagram of a thermostated block designed to hold a capacitance humidity sensor. Thermostating can be achieved with a heater pad pressed to the block and a temperature controller.

teresis. However, the bulk and cost of such additions reduce the advantages of having a small inexpensive sensor.

8.5 CALIBRATION OF WATER VAPOR SENSORS

Calibration of humidity sensors requires known humidities to be established. Two general approaches are available and adaptable for field use: (1) obtain equilibrium humidities over saturated salt solutions or hydrated salts or (2) condensation of humidified air to a known dew point. Additionally, other humidities can be obtained by mixing dry air with air of known humidity using mass flow controllers (see Chapter 11).

8.5.1 Salt solutions and hydrated salts

Saturated salt solutions, made by adding enough of the salt to distilled water so that crystals remain in the bottom of the container, can be used to obtain a wide range of relative humidities. Table A13 in the Appendix gives the relative humidities and vapor pressures as a function of temperature for a series of salts covering nearly the full range of relative humidities. The temperature coefficient of the equilibrium relative humidity is quite small in most cases but temperature gradients or changes are important because they prevent establishment of a true equilibrium. Any impurities in either the salt or the water will give an incorrect relative humidity. The major disadvantage of this technique is that the container must be closed and thermally insulated in order to establish an equilibrium. Thus, either the sensor must be removed from the instrument and sealed into the container or the container sealed on to the porometer. After sealing, at least 5–10 min are required to establish the equilibrium.

Hydrated salts may also be used to establish known vapor pressures in an air stream. The water vapor pressure in equilibrium with a

salt hydrate pair is a function of the nature of the hydrate pair and the temperature, but not of the relative proportions of each hydrate. Parkinson and Day (1981) have used this principle to develop a calibration system in which the salt is ferrous sulfate heptahydrate ($\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$). With dehydration it undergoes a transition to $\text{FeSO}_4 \cdot 4\text{H}_2\text{O}$ and, if allowed to come to equilibrium, establishes a dew-point temperature given by:

$$T_d = 1.134 T_s - 11.6 \quad [^\circ\text{C}] \quad (8.15)$$

where T_d is the dew-point temperature and T_s is the temperature of the salt.

A calibration system utilizing this principle is commercially available from the Analytical Development Company (UK; model WG600) but requires line power for heating the columns, limiting its usefulness under field conditions. A calibration system can be constructed by filling glass or plastic columns with $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$ and then passing an air stream through the columns. The air stream entering the column should be drier than the equilibrium dew point in order to establish the correct equilibrium. Moreover, the column volume needs to be sufficiently large and the flow slow enough that both thermal and vapor pressure equilibria are established. The temperature can be measured with a thermocouple or a thermometer embedded in the salt crystals of the last column. The main disadvantages of this method are that care must be taken to assure that a vapor pressure equilibrium is established and only one vapor pressure can readily be obtained without fairly elaborate systems for changing temperature. However, they can be used in conjunction with gas-mixing systems to obtain different vapor pressures.

8.5.2 Condensation techniques

The second approach to establishing humidities for calibration is by condensing water vapor out of a saturated air stream to a known dew point. The vapor pressure in the

air stream can then be calculated with sufficient accuracy from the relationship:

$$v_w = \exp(52.57633 - 6790.4985/T - 5.02808 \ln(T)) \quad [\text{kPa}] \quad (8.16)$$

where T (K) is the dew-point temperature and v_w is the water vapor pressure in kPa (Campbell, 1977). If a calibration of a relative humidity sensor is desired then it is also necessary to measure the temperature at the sensor and to calculate the saturation vapor pressure at this temperature. Also, pressure measurements must be made if there is more than a 0.5 kPa or so difference in the system or if it is significantly above atmospheric pressure. The humidifier can be a gas washing bottle or a column lined with water-saturated filter paper. The temperature of the humidifier must clearly be greater than that of the column. Because of the evaporative cooling in the humidifier, it is often better to use several in series so that the last one remains warm. Condenser systems incorporating thermoelectric cooling to set the dew-point temperature are available from H. Walz (West Germany) and W. Gries (West Germany). A simple but functional design is discussed in Chapter 11. An even simpler column which is suitable for calibrations can be constructed from copper tubing immersed in an insulated flask containing water of the desired dew-point temperature (Fig. 8.6). Heat transfer between the copper and the air is quite efficient so that only a short length of tubing is adequate for low to moderate flows. By adding water of different temperatures, different dew points can be obtained. Temperatures in the flask change only very slowly so that over the time required for the calibration, the dew point is essentially constant. The water should be agitated periodically to prevent development of any thermal gradients. The dew-point temperature can be measured with a thermocouple placed in the outlet below the water level in the thermos. The flows should be kept low so that pressure drops are small, otherwise, the pressure

must be measured with either a simple water manometer or an electronic pressure transducer and the humidity corrected for the change in pressure. While this condensation system is very simple, it functions remarkably well and is essentially trouble-free. The only difficulty is that if drops of water inadvertently get into the outlet tubing, which can occur if too much condensate collects, they will obviously add water vapor.

8.6 SYSTEMS FOR MEASURING TRANSPIRATION AND LEAF CONDUCTANCE

The most widely used instruments for measuring stomatal conductance are diffusion porometers. In principle, all diffusion porometers measure transpiration which is then used to derive a value for the stomatal conductance. Three general types of porometers are in wide use: (1) transient porometers which measure the rate of humidity increase within a closed chamber attached to the leaf, (2) null-balance porometers where the humidity is held constant by matching a flow of dry air into the chamber so that it balances the water vapor being lost from the leaf and (3) constant-flow porometers where the steady-state increase in vapor pressure occurring after the leaf is enclosed in the chamber is measured.

8.6.1 Transient porometers

The earliest porometers were of the transient type which was first developed by Wallihan (1964). Various modifications to the basic design have been made over the years (Kanemasu *et al.*, 1969; Byrne *et al.*, 1970; Turner and Parlange, 1970; Stiles *et al.*, 1970) but the principle of operation has remained essentially the same. A small chamber containing a humidity sensor is clamped on to the leaf surface and either the time required for an increase in humidity between two preselected levels or the change in humidity

for a given time interval is determined. Unstirred porometers relying on diffusion of water vapor from the leaf to the sensor are dependent on the geometry of the chamber, sensor and leaf. They cannot be used with conifers or with leaves that do not completely cover the chamber aperture. Ventilated transient porometers such as those developed by Kaufmann and Eckard (1978) and Körner and Cernusca (1976) can be used with a wider variety of plants but are more difficult to calibrate.

While it is theoretically possible to calculate a stomatal conductance from the rate of increase in humidity in a transient porometer, the response time of the sensors and absorption of water vapor within the chamber necessitate an empirical calibration. Typically a flat plate containing fields of pores and backed with wet filter paper is used in place of the leaf. The diffusion resistance of the pore fields can be calculated from the size and number of pores. Since water vapor absorption and the sensor characteristics are dependent on temperature, calibrations must be carried out over a range of temperatures similar to that present when the porometer is to be used. During the calibration, care must be taken so that the filter paper is not so wet that water is squeezed into the pores or so dry that an additional resistance is present. Ventilated porometers cannot be calibrated in this manner because strictly diffusional conditions may not hold within the pores. Instead, a wet surface such as scintered glass plate or filter paper connected to a glass capillary can be used to mimic transpiration (Körner and Cernusca, 1976). Movement of a bubble along the capillary can be used to calculate the rate of evaporation into the chamber. Transient porometers are relatively simple and comparatively inexpensive, but the laborious calibration, temperature response and susceptibility to drift and errors associated with water vapor sorption cause many problems. Certainly, the earlier and simpler designs are not at all reliable and

should be avoided. The design of Stiles *et al.* (1970) overcomes some of the limitations and an improved version is manufactured by Delta T Devices (model Mk II) in Great Britain. The Delta T Device model Mk II porometer has a small molded polypropylene chamber enclosing a capacitance-type humidity sensor which is clamped on to the leaf surface. The humidity is automatically cycled over preselected ranges via silica gel desiccant and a pump, which is turned on to lower the humidity and then off to allow the humidity to rise because of transpiration. The time for the humidity to increase between two preselected levels (the transit time) is measured and displayed. Generally four to five cycles, each lasting typically less than 5 s are required to obtain repeatable transit times. The improvements in performance of this porometer over earlier transient porometers result from the cycling until repeatable transit times are achieved, the use of polypropylene and other materials to minimize vapor sorption, and the use of a capacitance-type humidity sensor.

8.6.2 Null-balance porometers

The null-balance porometer, first developed by Beardsell *et al.* (1972), uses a flow of dry air through the chamber to balance the transpiration rate of the leaves and therefore maintain a steady-state humidity in the chamber (Fig. 8.7). Because the humidity of the entering air is known (usually 0% or very close to 0% relative humidity) it can be shown that under isothermal conditions, determination of g_w requires only a humidity measurement of the air within the chamber, the flow rate of dry air entering the chamber and the leaf area. In practice, however, conditions are not isothermal so that leaf and air temperatures must also be measured.

The null-balance porometer has several inherent advantages over transient porometers. Since a steady-state condition can be achieved at a humidity similar in most cases to ambient levels, errors due to water vapor

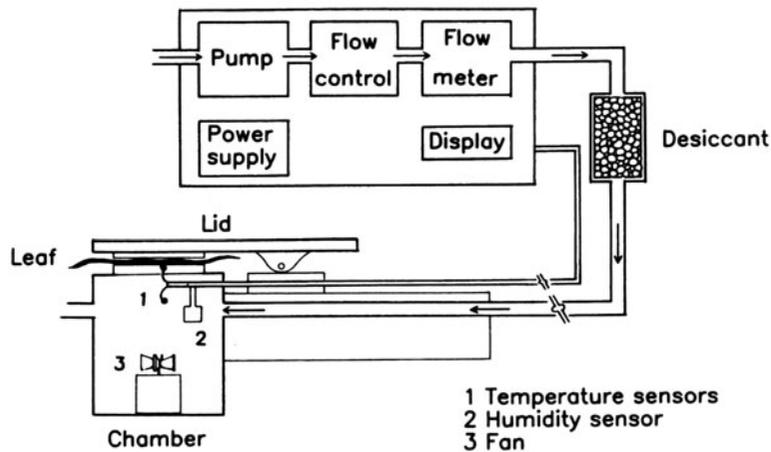


Fig. 8.7 Block diagram showing the components of a null-balance porometer.

sorption can be minimized. The calibration is also much easier since the humidity sensor can be calibrated at constant humidity levels over saturated salt solutions or with air of a known dew point. The flow meter can also be fairly easily calibrated (see Chapter 13), or at least checked for accuracy.

A commercially available null-balance porometer (model LI-1600) is available from LICOR Inc. (USA). This instrument utilizes a capacitance-type (Vaisala) sensor mounted in a ventilated chamber. The apertures are interchangeable so a wide variety of leaf shapes and sizes can be accommodated. For broad leaves, the surface not enclosed by the porometer is uncovered, which facilitates energy exchange and avoids over temperatures (Schulze *et al.*, 1982). An external shroud with a second fan helps to maintain the chamber temperature close to ambient air temperatures. A flow of dry air is supplied to the chamber via a pump and desiccant tubes containing silica gel, and the flow rate is measured with an electronic mass flow meter. An electronic bleed valve system connected to a feedback circuit regulates the flow into the chamber so that steady-state humidity is

maintained at a level preselected by the operator. In practice, the ambient humidity is usually measured with an open chamber and selected as the set point. Other humidities can also be selected if necessary provided that the instrument is conditioned for a while at this humidity. Manual adjustment is only required to bring the flow into the range where the automatic valve can control properly. A microprocessor-based data-acquisition system within the control console measures the signals from the leaf and air temperature thermocouples, the flow meter and humidity sensor and provides a readout of stomatal conductance on an LCD display. Measurements of stomatal conductance generally require between 15 s and 1 min with this porometer. A rechargeable battery allows 5–6 h of continuous use under field conditions.

Transpiration measurements in the LICOR 6200 photosynthesis system (see Chapter 11 for a full description) are intermediate between a transient and a null-balance system. While the flow in this instrument can be set so that the relative humidity is maintained constant, in practice, it usually increases or decreases. Thus the calculations are based

both on the transient rate of increase in the relative humidity and the flows out of the chamber to the CO₂ analyzer.

8.6.3 Constant-flow porometers

In contrast to the null-balance porometers where the flow is varied to achieve a compensation of the vapor added by transpiration, several porometers have been developed that maintain a constant flow of dry gas through the chamber (Parkinson and Legg, 1972; Day, 1977). After a steady state has been achieved, the resulting humidity is measured. The major disadvantage of this type of porometer is that the leaf and chamber may be exposed to quite different humidities from the ambient levels, depending on the flow through the system. If the change in vapor pressure is large, absorption or desorption of water may occur, leading to errors in the conductance measurements, or stomata may respond to the changed vapor pressure.

Recently, porometers utilizing a constant-flow principle for the simultaneous measurement of CO₂ and H₂O exchange have become available in which a constant flow rate of the ambient air is maintained through the chamber during the measurement, and, for transpiration, the difference in vapor pressure of the entering and exiting air is measured (Fig. 8.8). Flows through the chamber must be kept fairly high so that there is not an excessive depletion of CO₂ or increase in vapor pressure. Consequently, the vapor pressure difference between the reference and sample is kept small and an infrared analyzer is required in order to obtain sufficient accuracy. A CO₂/H₂O porometer of this type was developed by Schulze *et al.* (1982) and is available commercially from H. Walz (West Germany). The chamber is similar to that of the LI-COR 1600 porometer, but an air stream of constant flow is passed through the chamber and monitored with a multi-channel gas analyzer (Binos). The thermo-

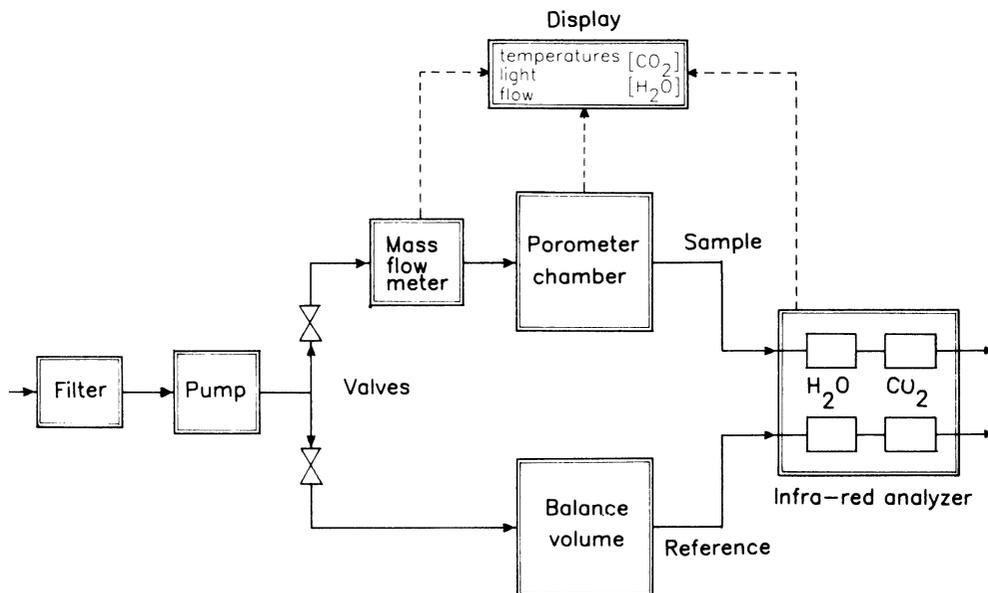


Fig. 8.8 Block diagram showing the components of a constant-flow porometer.

couple and Vaisala humidity sensor in the chamber determine the leaf-air vapor pressure gradient. A similar system manufactured by W. Gries (West Germany) uses a four-channel Binos gas analyzer to obtain the absolute and differential CO_2 and H_2O pressures and incorporates a Sharp computer for data processing. Both systems can be equipped with temperature-controlled cuvettes, CO_2 -gas mixing systems and vapor condensers, and thus have considerable flexibility. They have the great advantage of providing both CO_2 and H_2O exchange measurements, which for many studies is essential. The disadvantages are that they are quite expensive and considerably less portable than, for example, a LI-COR 1600 porometer. Details of systems designed to measure both CO_2 and H_2O exchange are given in Chapter 11.

8.6.4 Comparisons of porometer types

Null-balance porometers are more complex and therefore more expensive than transient porometers. Constant-flow porometers are less complex than null-balance porometers but the requirement for an infrared analyzer for the $\text{CO}_2/\text{H}_2\text{O}$ porometer makes it considerably more expensive. However, constant-flow porometers are also less portable than either transient or null-balance porometers. Both null-balance and constant-flow porometers are in effect equivalent to a leaf chamber and the calculated conductances in both are based on mole fraction gradients of water vapor and the measured transpiration rates. Thus, the estimates of gas fluxes and conductances are derived from first principles. Conductance estimates with the transient porometer are based on a comparison with the calculated conductance of the calibration plate. With care this can provide a standard but it may not be directly comparable with diffusion through stomata.

Null-balance porometers function best at high conductances where the balancing flow is high whereas for transient porometers, the

time response of the sensor, timing errors and failure to establish uniform humidity gradients within the chamber cause them to be less accurate at high conductances. Because of the greater inherent accuracy of the infrared analyzer as compared with thin-film capacitance sensors used in null-balance porometers, continuous-flow porometers are potentially the most accurate. In null-balance and continuous flow porometers, the error in the humidity measurement affects both the estimate of the vapor pressure gradient and the transpiration rate. For conductance measurements the effect of the error enters twice in the same direction into the calculations. An error analysis of the equations used to calculate g_w for a null-balance porometer shows that a 1% humidity error gives a 4% error in g_w at a relative humidity of 50% (Campbell, 1975). The error increases dramatically at humidities below 20% because of error in the transpiration term and above 80% because of error in the gradient. If the real error in a humidity sensor is 4%, which is possible because of drift in thin-film capacitance detectors that are not frequently calibrated, then the error in g_w would be 16%. Errors in transient porometers are more difficult to specify because it depends on the calibration standard; where the calibration is based on a measured evaporation rate using for example a microcapillary pipette, a 1% humidity error has less than a 2% effect on the calculated g_w below 50% relative humidity. Above 80% relative humidity the error rises dramatically. In practical terms, however, the slight advantage of dynamic over null-balance porometers with regard to dependence on the humidity sensor accuracy is outweighed by other errors introduced in the calibration. The use of porometers at high humidities (i.e. greater than 75% as is often found in tropical or boreal forests) presents special problems. The potential errors shown above are compounded by poor performance of thin-film capacitance sensors at high humidities. In these circumstances the constant flow porometer has

inherent advantages, although it should be recognized that all conductance estimates are subject to more error under these conditions because of the low rates of transpiration and low vapor pressure gradients. If a null-balance porometer such as the LI-COR 1600 is to be used in high-humidity environments, then it is best to store the head at lower humidity and use a lower humidity set point during the determinations.

One of the most critical factors in all porometers is temperature. The calibration of transient porometers assumes equal leaf and air temperatures; if they are not, the errors can be substantial (Morrow and Slatyer, 1971). Unfortunately, the leaf temperature thermistor is typically mounted in the foam gasket surrounding the aperture away from the evaporating leaf surface. Consequently, it is very difficult to tell if the leaf and air temperatures are the same. Leaf and air temperatures are measured separately in the LI-COR null-balance porometer. In all porometers, a changing temperature after closure will result in absorption or desorption of water vapor in the chamber that will be added to or subtracted from the true transpiration rate. The problem is minimized by using materials that have low water absorbances (Bloom *et al.*, 1980; Dixon and Grace, 1982; also, see Chapter 11) but it cannot be eliminated. If the porometer is moved from a cool to a warm location or into a growth chamber just prior to use, significant errors could result. Also, in a null-balance porometer such as the LI-COR 1600, an increasing air temperature causes a decreasing relative humidity and consequently causes the flow to decrease as the controlling system attempts to adjust relative humidity back to the set point. Because flow is the primary input for all rate calculations, conductances will be underestimated. These problems are most severe for low conductances. The best way to minimize temperature problems is to keep the porometer in the shade between measurements so that it will be close to air temperature.

Because of the differential water vapor measurements made in the constant-flow porometer, it should be less subject to these temperature errors.

8.7 WHOLE-PLANT MEASUREMENTS OF TRANSPIRATION

8.7.1 Extrapolation from porometry

One of the most tempting approaches to estimating whole-plant transpiration is to extrapolate from porometer measurements on single leaves to the canopy. It must be made quite clear, however, that this is not easily accomplished. Mainly because of boundary layer conditions, transpiration rates measured in a porometer will be different from that of a leaf transpiring under undisturbed natural conditions. Consequently, the only completely valid approach is to calculate transpiration from conductances measured with a porometer and vapor pressure gradients determined independently from leaf temperatures and the ambient vapor pressure of leaves in their natural position. Boundary layer conductances should be determined (see Chapter 4) and reciprocally added to the stomatal conductances, since they will be quite different for leaves in the chamber as compared to natural conditions, especially for large leaves. This requires estimates of wind speed within the canopy. In addition, stomatal conductances, leaf temperatures, vapor pressures and wind speeds must be known in different canopy layers. The problem is less acute for needle-leaved species, such as conifers, than for broad-leaved plants because of the high boundary-layer conductances and close coupling to air temperature. The extrapolation of porometer transpiration data may be justified when: (1) the leaves are small, (2) the aerodynamic (canopy) boundary layer resistance is low (Jarvis, 1985) so that vapor pressure and wind gradients are small, and (3) the leaf area distribution among the

different vapor pressure regimes in the canopy are known. Under these special conditions an extrapolation was successfully made for *Picea* and *Larix* by Schulze *et al.* (1985), but this may not be possible for conditions of lower canopy roughness (Jarvis, 1985).

Even when the extrapolation is possible, the requirement for sufficient sampling dictates that measurements will be achievable for only one or a very limited set of conditions. Thus extrapolation to daily or seasonal transpiration requires simulation modeling. Models incorporating stomatal responses to environmental variables have been developed for different species (Thorpe *et al.*, 1980; Küppers and Schulze, 1985). To scale up from a conductance model of this type, additional models of radiation penetration into the canopy and leaf microenvironment are required but are generally difficult to adjust for a specific situation. Caldwell *et al.* (1986) have used this approach to predict daily and annual totals for *Quercus coccifera* canopies in a Portuguese macchia. A major difficulty is validation of the models; Caldwell *et al.* used the good agreement between soil water use and predicted transpiration as a validation. Models of this type may be most useful for examining the consequences in a hypothetical sense of changes in canopy structure such as leaf area index or leaf angles on whole-plant water use.

8.7.2 Xylem flow measurements

The most immediate way of determining the total water flow through a plant is to measure the amount of water passing through the stem between the root system and the canopy. Because the opposite flow in the phloem is so much smaller than the xylem flow, the latter can be equated with the total flow. Measurements in intact plants were first attempted by Huber and Schmidt (1932), who developed the 'heat pulse method', which measures the velocity of the water flow in the xylem. In

order to calculate the total amount of water, the actual conducting area must be known, which is generally impossible, since it is not known which vessels participate in transport of water. To overcome this limitation, a 'heat balance' method was applied by Vieweg and Ziegler (1960) and further developed by Čermák *et al.* (1973), using the specific heat capacity of water for keeping a temperature gradient constant, allowing long-term and continuous observations of xylem flow in the field.

(a) Determination for xylem flow velocity

The xylem flow velocity, V , can be determined by inserting a heating-device in a certain distance, D , below a temperature sensor (commonly a thermocouple) in the hydro-active xylem. The velocity is then determined by measuring the time interval, t , between a heat-pulse applied by the heating device and the detection of a temperature increase at the temperature sensor.

$$V = \frac{D}{t} \quad (8.17)$$

If the water content of the conducting xylem vessels is known, one can then calculate the mean rate of water transport through the measured section of the stem. However, this calculation contains several unknowns. First, the determination of the amount of conducting xylem area is difficult to determine even after cutting the stem and examining its cross-section. Because of wall friction, only part of the vessel cross-section is actually conducting (Čermák *et al.*, 1973). Attempts to estimate it have been made by coloring the xylem during transpiration with dyes (Čermák *et al.*, 1984) but the pattern which emerges is very complicated. The xylem flow can vary within a great range from young to old conducting vessels. But even these calculations by Čermák *et al.* (1984) show that not all vessels contribute to the flow, although the total area may be dyed. Moreover, xylem vessels often ana-

stomose, making it difficult to determine the true distance between the heat source and the temperature sensor.

(b) Measurement of xylem sap mass flow

To overcome the problem of determining the effective area of the xylem, a steady-state mass flow technique, using the specific heat capacity of water C_w (4186.8 J K⁻¹ kg⁻¹ at 15°C) can be used. There are two principal methods of measurement: constant heating and null balance.

Constant-heating method. In this method xylem water is permanently heated with a constant amount of energy. The increase of the xylem sap temperature at a selected distance above the heating point can be used to calculate the mass flow of water through the xylem vessels. Although it is simple to install a constant-heating device and to measure the temperature difference between the point of heating and the higher point, problems can occur when xylem flow is low or stops during the night, leading to low removal of heat from the heater and the potential for xylem heat injury. Problems arise also at high mass flow rates occurring when transpiration rates are high which result in small temperature increases and poor signal resolution.

Constant-heating methods are described for herbaceous species with small stem diameters by Sakuratani (1981) and for trees by Granier (1985). In the instrument of Granier (1985, 1987) the xylem is heated with constant energy supply at one point by a small cylindrical probe containing a resistance wire heater and a thermocouple which is inserted 2 cm into the stem. Approximately 10 cm downstream, a second probe with a thermocouple but no heater measures the temperature. The temperature difference between the two probes is strictly influenced by the sap flow density around the heating probe. The sap flow (F , m³ h⁻¹) of the tree can be calculated as follows:

$$F = 0.4284Sa \left(\frac{T_m - T_d}{T_d} \right)^{1.231} \quad (8.18)$$

Where Sa is the sapwood area at the heating probe level (m²), T_m is the maximum temperature difference (K) obtained when sap flow is zero (measured at the end of the night when the xylem water potential is high and there is no water vapor pressure difference between plant and atmosphere), and T_d is the temperature difference between the two probes (K). This method needs calibration of each new installed device for the value of T_m , which depends on the thermal characteristics of the wood. Additionally the whole device must be thermally insulated to minimize temperature drifts due to direct solar radiation striking the stem or wind. In contrast to the heat pulse method, the calculation is not dependent on knowledge of the conducting area, since a mass flow and not a velocity is the basis of the measurement.

Null-balance method. A steady-state null-balance method maintains a preselected temperature difference of between 1 and 2 K between the reference temperature measured downstream from the heating point and temperature measured by a sensor at the point of maximum heat input. The electric energy is controlled such that the temperature difference is held constant independent of the xylem flux. The advantage of this system is that the amount of energy input to the heaters is directly proportional to the mass flow of water in the xylem irrespective of area and that no tissue overheating occurs at low xylem flux.

The main practical problem in the steady-state system is the application of an even temperature field to the whole conductive xylem area. For herbaceous species or small woody branches, a resistance wire spiral wound around the shoot and insulated against heat loss to the atmosphere is normally sufficient. This principle is described by

Schulze and Fichtner (1988) and was applied successfully to herbs and lianas.

For large trees, it is practical to heat only small sections of the sapwood, which can be done for example on opposite sides of the tree. Moreover, the heat cannot be supplied externally because of the insulating effects of the bark. In this case, a resistance-wire-heater probe or an alternating current (AC) supplied via electrodes inserted in the xylem can be used. Current flows between the electrodes, which remain cold, but because the xylem sap through which the current passes has a resistance, it is heated up. The AC current avoids problems with ion migration in the xylem sap. This principle of heat balance xylem sap measurements was first applied by Vieweg and Ziegler (1960) and was further developed by Čermák and Kucera (1981) by adding thermal compensation for natural temperature gradients occurring at the measuring point. The measuring device, which is commercially available from S.E.P. Gröger (West Germany), consists of five vertical stainless-steel electrode plates which are inserted in parallel into the xylem at a spacing of about 20 mm. A network of four thermocouple pairs inserted to various depths between the electrodes (the point of maximum temperature) measure the difference in temperatures with reference to points 10 cm below the plates. There is a controller circuit that regulates the power applied to the electrodes so that a constant temperature gradient (usually 1–2°C) is maintained. The power applied to the electrodes is recorded. Measurements from the eight thermocouples are also used to compensate automatically for thermal gradients caused by wind or solar radiation. In addition, the whole trunk section is covered with foam insulation and aluminium foil to minimize these externally imposed gradients. The depth of insertion of the thermocouples and electrodes depends on the diameter of the sapwood area, with the objective being that heating occurs across the entire hydroactive xylem segment. The cal-

culatation of xylem sap mass flow requires an estimate of the total conductive xylem area at the electrode level and the proportion which is heated by the electrodes. This can be obtained by analyzing a stem core. The total xylem mass flow (F_m , kg h⁻¹) is given by the difference of the measured mass flow without compensation of the heat losses of the measuring point Q and the fictive mass flow Q' which can be obtained during night when actual xylem flow is supposed to be zero.

$$F_m = Q - Q' \quad (8.19)$$

Both the recorded mass flow Q and the fictive mass flow Q' can be calculated according to the following equation:

$$Q = \frac{Pk}{C_w T} \quad (8.20)$$

where P is the power input (J s⁻¹) into the heating electrodes, C_w is the specific heat capacity of water (J K⁻¹ kg⁻¹), T is the temperature difference (compensated against drifts) between the heated and the unheated part of the xylem in K. The dimensional constant, k , relates the section flux to the total circumference:

$$k = \frac{\theta}{d(n-1)} \quad (8.21)$$

where θ is the circumference (m) of the woody part of the tree at the measuring device, d is the distance between the electrodes (m) and n is the number of heating electrodes.

This measuring system has been used for xylem flow measurements in a variety of conifers and deciduous trees. The device, once installed, can monitor continuously the xylem mass flow for some months without problems. Changes in water flow on a scale of minutes can readily be observed. For

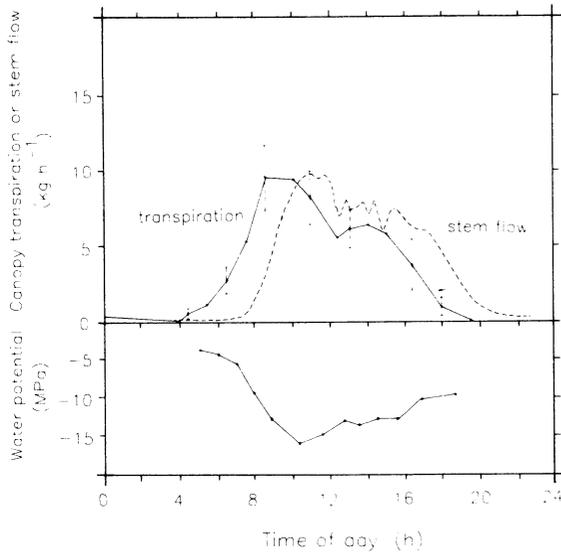


Fig. 8.9 The daily course of transpiration (solid line) of a *Larix* hybrid tree canopy, as calculated from porometer measurements and canopy leaf area, and the xylem water flow (dashed line) measured with the heat balance method of Čermák *et al.* (1983). Stem flow lags behind because of the capacitance of the stem. In the morning the water content of the stem declines because transpiration exceeds water uptake while in the late afternoon the stem is recharged. Redrawn from Schulze *et al.* (1985).

example, Schulze *et al.* (1985) measured xylem flow of *Larix* and *Picea* trees and compared it to estimates of transpiration derived from a porometer and a controlled climate chamber (Fig. 8.9). Xylem flow can be seen to lag behind the canopy transpiration estimates from the porometer because of the capacitance of the stems and foliage, but on a daily basis there was close agreement (77 kg day^{-1} for the xylem flow and 75 kg day^{-1} for the extrapolation from the porometer). Comparisons with gravimetric water loss measurements suggest that the accuracy of the technique is around 10% (Penka *et al.*, 1979).

The major difficulties with the technique arise because of poor insulation and temperature gradients and from the accuracy of the measurement of the temperature difference. If the difference is controlled at a set point of

1 K and temperatures are measured to 0.1 K, then there is a 10% uncertainty in the flow measurement. Insulation can be applied effectively to trees but not easily to herbaceous plants or small branches. Measurement with small herbaceous plants is further complicated by temperature differences between the soil and air, which may then result in a temperature gradient in the xylem. Errors may also arise if the stem is not heated homogeneously. For large trees there is little problem since the electrodes can be spaced at equal distances. However, for small trees the electric field density between electrodes may not be constant. Also, in systems heated by wire wound around the stem, water flowing in the center may not reach the set point at high flow rates, whereas that close to the bark may rise above the set point.

8.7.3 Lysimeter measurements

For monitoring the total water loss of a potted single plant within a brief time interval the change in total weight is often used in laboratory experiments as the most direct and exact method of whole plant water loss. The same principle can also be used in the field, but it needs extensive preparations and control. After installation it is limited to monitoring at most a few individuals. Regardless of the restrictions it is a valuable possibility to measure transpiration and to compare these results with other methods for estimating, modeling or measuring transpiration of individual plants although it is much more expensive than measuring xylem flow directly. But in contrast to the xylem flow measurement the lysimeter measures the total mass changes of the root-stem-canopy system to the environment. It measures uptake and evaporative water loss which bypasses the plant. A disadvantage is that the root system and the soil structure invariably undergo some disturbance.

Commonly a lysimeter is installed by isolating a section of undisturbed soil which is

rooted by a single plant in the case of trees or by a plant population in the case of crops from the circumfering soil. The soil block is enclosed in a container, sitting on a balance. For bigger plants, e.g. trees, the appropriate balance device is a ring of elastic tubes at the bottom of the soil container. The weight is measured by filling the tubes with airless water or oil and applying a hydrostatic pressure column to compensate the container weight. Pressure changes of the tubing system indicate weight changes. The hydrostatic balancing has a series of advantages. The total weight of the container can reach over 25 tons for trees with root systems. The accuracy is only dependent on the accuracy of the pressure sensor. The instrumentation with tubes also needs only a small space for installation below the lysimeter soil container.

For measuring the transpiration of the plant under field conditions, several parameters influencing the weight of the container have to be taken into account. Weight losses can occur due to transpiration water loss (via stomata, cuticle and bark), evaporation from the soil, respiration of tissue and soil and biomass loss (litter fall and loss of twigs or bark). Weight gain can occur from water uptake by rainfall, fog interception or snow deposition and from pressure changes in the surrounding soil. For a longer period of time also the carbon-uptake via photosynthesis has to be considered. The main problems are related to the water content of the soil in the container. Since the free capillary exchange of ground water is stopped by the container walls, water can accumulate during rainy periods or the soil dries much faster than under normal conditions.

By installing a separate drainage/watering system by protecting against rain and litter fall, factors influencing the total weight changes can be eliminated, leaving the net plant water losses over short periods. But in these cases the system is by no means 'natural'. Depending on the sensitivity of the installed pressure sensor, the accuracy of

such lysimeters can reach values of 0.06 to 0.02 (mm water column per m² soil surface) (van Bavel and Meyers, 1962; Fritschen *et al.*, 1973). Using lysimeter systems in combination with photosynthesis and tissue respiration measurements on the one hand and soil water potential measurements on the other provides a complex approach to water dynamics with larger plants. However, they are clearly expensive, difficult to install and present many technical and logistical difficulties. For many purposes, the use of xylem flow devices is a satisfactory alternative.

Still lysimeters play an important role in estimating the water balance and evapotranspiration, but this may also be done by water budgets and neutron probe measurements in a natural soil profile. Furthermore, lysimeters may be used as 'pots' in order to define the root development of plants if root studies are desired, but in this case a weighting installation is not necessary.

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