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7

Temperature and energy budgets

James R. Ehleringer

7.1 INTRODUCTION

Temperature is of fundamental importance in affecting rates of metabolic activity in plant tissues. In this chapter, we will focus on methods for temperature measurement under field conditions and on the energy budget equation, which basically describes the influences of abiotic/biotic factors in affecting a deviation in plant tissue temperature from the surrounding ambient air temperature. As such the primary emphases of this chapter will be to describe (1) the principles behind the energy budget approach, (2) the leaf parameters which will influence leaf energy balance and thus need to be measured, (3) how leaf, air and soil temperatures are most commonly measured and (4) the precautions necessary to minimize errors in leaf, air and soil temperature measurements.

Although temperature is the emphasis of this chapter, a number of topics will not be considered because of space limitations. These include factors influencing air/soil temperature profiles (such as Richardson's numbers and damping depths), Bowen ratios and degree-day concepts. These as well as other microclimatological topics are discussed in depth in recent texts by Monteith (1973), Campbell (1977), Jones (1983) and Rosenberg *et al.* (1983).

7.2 ENERGY BUDGET APPROACH

All organisms and objects interact with their physical environment through energy-exchange processes. For leaves these processes include radiation absorption, reradiation, convection and transpiration. Different leaf temperatures arise because of a combination of changes in the air temperature surrounding the leaf and changes in leaf energy balance. An understanding of leaf energy balance or, as it is more often called, the energy budget equation, will allow the quantitative prediction of how leaf temperatures will change in response to abiotic factors such as solar radiation intensity and wind speed or to biotic factors such as leaf angle and stomatal conductance to water vapor.

7.2.1 Energy budget equation

At equilibrium, the rate of energy absorbed by a leaf equals the rate of energy loss. If these energy components are not in balance, then leaf temperature will change (increase or decrease) until an equilibrium situation is achieved. Because of the very high surface to volume ratios of most leaves, energy exchange is rapid and equilibrium in energy exchange is usually approached within a matter of seconds.

Absorbed radiation = reradiation + convection + transpiration (7.1)

While this equation describes the major components of energy exchange in leaves, it ignores three other possible forms of energy exchange: energy fixation into stable carbon compounds during photosynthesis, energy production via respiration, and energy transfer via conduction. These three components of the leaf energy budget equation can usually be ignored because they are of low magnitude in comparison with the major forms of leaf energy exchange as shown in Equation 7.1.

Before proceeding to describe the energy budget equation further, it may be useful to describe briefly the energy-exchange processes being considered. Radiation absorption involves the absorption by leaf tissues of both shortwave radiation (solar radiation) and phase. This state conversion requires a significant amount of energy.

Equation 7.1 can be expanded for a single leaf to

$$aS + \epsilon IR = 2\epsilon\sigma(T_l + 273.15)^4 + 2h_c(T_l - T_a) + 2L(\rho_l - \rho_a)/(r_s + r_a) \qquad (7.2)$$

where a is the leaf absorptance to total solar radiation (400–3000 nm), S is the total amount of direct, diffuse and reflected solar radiation incident on a leaf, ϵ is the emissivity of the leaf to infrared radiation, IR is the sum of infrared radiation from the ground and the sky, σ is the Stefan–Boltzmann constant (5.67×10^{-8} W m^{-2} K^{-4}), T_l and T_a are the leaf and air temperatures, h_c is the convection coefficient, L is the latent heat of vaporization (2441 J g^{-1} at 25°C), ρ_l and ρ_a are the water vapor densities of the inner leaf air spaces and the outside air, and r_s and r_a are the stomatal and boundary layer resistances (inverse of the conductances) to water vapor transfer. Note that the factor two appears in several places in Equation 7.2. This is because energy is being absorbed and lost by both upper and lower leaf surfaces. The leaf temperature can be solved for iteratively using the previous equation or by using a linear solution (Miller, 1972):

$$T_l = T_a + \frac{E_{abs} - \epsilon\sigma(T_a + 273.15)^4 \times (L)(\rho_{s,ta} - \rho_a)/(r_l + r_a)}{4\epsilon\sigma(T_a + 273.15)^3 + h_c + (L)(d\rho/dT)/(r_l + r_a)} \qquad (7.3)$$

longwave radiation (sky and terrestrial infrared radiation). Reradiation is the process by which longwave radiation is reemitted by leaves. Convection is a process by which heat is exchanged between the leaf surface and the surrounding bulk air masses through physical contact. Finally, transpiration is the process by which water moves by diffusion from the inner leaf surfaces through stomatal pores to the outside air. Although transpiration is a mass movement, energy is also being transferred because of the kinetic energy content of that water leaving and because water movement from the leaf involves a state conversion of water from liquid to a gaseous

where E_{abs} is one-half the total energy absorbed by the leaf (solar and infrared radiation), $\rho_{s,ta}$ is the saturated water vapor density at air temperature, and $d\rho/dT$ is the slope of the saturation water vapor density versus temperature curve at air temperature.

The linear solution of the energy budget equation is approximate and reliable when leaf and air temperatures do not deviate greatly from each other. However, as leaf temperature deviates from air temperature, the error in this linear solution will increase proportionally. Given the speed of today's computers, a more satisfying solution is to use the Miller linear solution to obtain the

approximate leaf temperature and then to iterate incrementally to the final solution (you specify the solution limits).

7.2.2 Leaf coupling factors

The linkages between leaf temperature and the physical environment as shown in the energy budget equation are made by leaf coupling factors. These coupling factors represent either physical properties of the leaf or are parameters based specifically on leaf characteristics. The interrelationships between energy exchange processes, environment, coupling factor and leaf properties are presented in Table 7.1. It is through changes in leaf coupling factors that plants adapt and adjust to different physical environments.

Leaf coupling factors involved with absorbed radiation are the leaf absorptance to total solar radiation and leaf emissivity. Since the molecular composition of leaves is essentially the same, there are only small differences in leaf emittance to longwave radiation (Table 7.2). However, large variations in leaf absorptances do occur and representative values and how they are measured are discussed in Section 7.7. Changes in leaf absorptance need not be the only mechanism for reducing the amount of solar radiation absorbed. An alternative would be to reduce the amount of solar radiation incident on the leaf. This can be accomplished by increasing the leaf angle or by orienting the leaf away from the sun. Methods for measuring leaf orientation and quantifying the total amount of solar radiation incident on the leaf are presented in Sections 7.5 and 7.6.

The stomatal and boundary layer resistances serve to regulate rates of water loss from the leaf and, therefore, provide the coupling for latent energy exchange. Stomatal resistance is a function of the diameter and density of stomatal pores. The boundary layer resistance depends in part on leaf size and shape and arises because of the presence of a thin layer of laminar air flow above the leaf which increases the path length for water vapor diffusion.

The convection coefficient for sensible heat transfer is related to the boundary layer resistance as

$$h_c = V/r_a' \qquad (7.4)$$

Table 7.1 Energy-exchange processes and leaf coupling factors. Based on Collier *et al.* (1973)

Energy-exchange process	*Environmental factors involved*	*Coupling factor*	*Organism properties involved in coupling*	*Organism response*
Convection	Wind speed, air temperature	h_c	Size of leaf, shape of leaf	Temperature
Evaporation (transpiration)	Wind speed, water content of air	r_a	Size of leaf, shape of leaf	Temperature, water loss
		r_s	Stomatal density, stomatal opening, cuticular resistance	
Reradiation	–	ϵ	Molecular composition	Temperature
Energy absorption	Solar	a	Leaf color, leaf orientation	Temperature, photosynthesis
	Terrestrial radiation	ϵ	Molecular composition	Temperature

Table 7.2 Emittances to longwave radiation for various materials determined at approximately 25°C. Data are from Birkebak (1966), Holman (1968) and Idso *et al.* (1969)

	Emissivity
Non-biological materials	
Brass (polished)	0.04
Brass (dull)	0.22
Brick	0.93
Copper (oxidized)	0.78
Glass	0.94
Iron (new cast)	0.44
Iron (oxidized surface)	0.80
Silver	0.02
Water	0.95
Soils	
loam	0.97
sand	0.95
Biological materials	
Animals	
Glaucomys volans (flying squirrel)	0.95
Peromyscus sp. (deer mouse)	0.94
Scalopus carolinensis (mole)	0.97
Sylvilagus floridanus (rabbit)	0.97
Leaves	
Gossypium hirsutum (cotton)	0.96
Nicotiana tabacum (tobacco)	0.97
Opuntia basilaris (cactus)	0.98
Phaseolus vulgaris (bean)	0.96
Populus fremontii (poplar)	0.98

where V is the volumetric heat capacity of air (the product of the heat capacity of air and the density of air) and r_a' is the boundary layer resistance for heat transfer (approximately $r_a^{1.5}$). A more detailed description of boundary layer and stomatal resistances and the procedures used to measure them are presented in Chapters 4 and 8 respectively.

7.2.3 Parameters to be measured for the energy budget equation

A number of parameters must be measured as inputs into the energy balance equation in order to calculate leaf temperature and transpiration rate correctly. These parameters and a sequence for their calculations are presented in Table 7.3. The measurements described in Table 7.3 allow the determination of the individual paths of energy absorption and loss by the leaf. However, for simulation or calculation purposes when leaf temperatures are not measured directly, it is more convenient to specify what environmental parameters must be measured in order to calculate the leaf temperature. In short, the environmental parameters are total solar radiation, total infrared radiation, wind speed and atmospheric humidity. The corresponding leaf parameters which must be measured are the total conductance to water vapor, absorptance and width.

7.2.4 Energy budget simulations

Perhaps the greatest utility of the energy budget equation is that it allows simulations

Table 7.3 Components of the energy budget equation and parameters that go into its calculation

Component	*Measurement*	*Instrument required*	*Chapter*	*Comments*
Solar radiation absorbed	Horizontal incident	Thermopile pyranometer	6	Measure on horizontal surface
	Diffuse	Thermopile pyranometer	6	Measure using shadow band
	Direct	Thermopile pyranometer	6	Subtract diffuse from solar total
	Reflected	Thermopile pyranometer	6	Measure by inverting pyranometer
	Total incident solar			Multiply direct by cos(*i*) for the leaf angle and azimuth. Then add the diffuse and reflected radiation
	Leaf absorptance	Integrating sphere	7	–
	Total absorbed solar			Multiply the total incident solar times the leaf absorptance
Longwave (infrared) radiation absorbed	Sky	Total radiometer or infrared thermometer	6, 7	Subtract solar from the total or calculate from the 'effective' sky temperature using the Stefan–Boltzmann equation
	Soil	As above or thermocouple		Subtract reflected solar from total measured with the total radiometer inverted or calculate from the soil surface temperature
	Total longwave			Add sky and soil together, then multiply by the emittance
Longwave (infrared) radiation loss	Leaf	Thermocouple or infrared thermometer	7	Calculate using Stefan–Boltzmann equation. Multiply by two to account for both surfaces. Then multiply by the leaf emittance
Latent heat loss	Leaf resistance	Porometer	8	Leaf resistance is inverse of leaf conductance
	Boundary layer to water vapor	Anemometer, ruler	4	Calculate boundary layer knowing leaf width and wind speeds using equations from Chapter 4
	Transpiration		8	Calculate from leaf and boundary layer resistances, and measure leaf to air water vapor gradient
	Latent heat			Multiply transpiration by latent heat of vaporization
Sensible heat loss	Leaf–air temperature difference	Thermocouples	7	Mostly easily measured using differential thermocouples
	Boundary layer	Anemometer, ruler	4	Calculate boundary layer knowing leaf width and wind speeds using equations from Chapter 4
	Convection coefficient			Divide volumetric heat capacity of air by boundary layer resistance
	Sensible heat			Multiply convection coefficient by leaf to air temperature difference

or calculations of what leaf temperatures and transpiration rates would be if one of the leaf or environmental parameters were to change. Such simulations are extremely valuable in assessing the sensitivity of leaf temperature and/or transpiration rate to changes in a single variable. The two simulations which follow illustrate the significance of changes in leaf coupling factors on the leaf energy budget and therefore on the temperature and water loss rates of the leaf.

Let us assume a reasonable set of environmental conditions such as might be observed at midday during a mild summer day: an air temperature of 25°C, a soil temperature of 30°C, a relative humidity of 30%, a wind speed of 1 m s^{-1}, and an incident total solar radiation load of 1000 W m^{-2}. Let us also assume reasonable nonstress values for the leaf coupling factors: a leaf width of 2 cm, a leaf conductance to water vapor of 0.2 mol m^{-2} s^{-1} on both upper and lower leaf surfaces.

Let us now ask the first question, how will leaf temperature and transpiration rate change solely as a function of changing leaf absorptance to total solar radiation? From Fig. 7.1, we see that leaf temperature will decrease from 27.6°C to 23.5°C when leaf absorptance decreases from 50% (typical for most green leaves) to 20% (quite reflective leaf surface). Solely as a consequence of this decrease in leaf temperature, the transpiration rate will decrease 28%, from 9.0 to 6.5 mmol m^{-2} s^{-1}.

For the second leaf energy budget simulation, let us ask how the temperature and transpiration rate of the green leaf will change as the leaf conductance is varied. For simplicity, the leaf conductance of the upper and lower surfaces will be equal, and the results are plotted as a function of total leaf conductance. From Fig. 7.1, we see that conductance changes have a profound effect on both leaf temperature and on transpiration rate. Leaf temperatures increase from 25.0°C to 33.9°C as leaf conductance decreases from 0.8 to 0.0 mol m^{-2} s^{-1}. At the same time, the transpiration rate decreases from 13.7 to 0 mmol m^{-2} s^{-1}, although the decrease is not linear with conductance because of the compounding effect of changes in leaf temperature with leaf conductance.

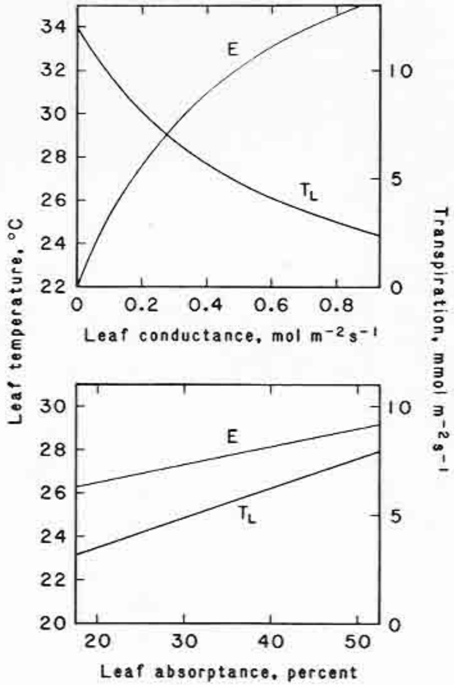

Fig. 7.1 Leaf energy budget calculations of the effects of changes in leaf absorptance (400–3000 nm) and in leaf conductance on leaf temperature (T_c) and transpiration rate (E). For these simulations T_a = 25°C, relative humidity = 30%, total solar radiation = 1000 W m^{-2}, leaf width = 2 cm, and wind speed = 1 m s^{-1}.

In both of these simulations it is clear that changes in the leaf coupling factors, even under moderate environmental conditions, will play a significant role in affecting both leaf temperature and transpiration rate. Thus, it should be evident that in approaching leaf temperature studies and in understanding the relationships between leaf and air temperatures, it is imperative to have a complete consideration of both the abiotic environment as well as the leaf coupling factors. Additionally, since air temperatures vary with height (see Section 7.3), the air and leaf temperatures should be measured at the same position within the microclimatic profile.

7.3 VARIATIONS IN AIR AND LEAF TEMPERATURES WITH HEIGHT

7.3.1 Horizontal variation and sample size

At any time there may be considerable spatial variation in air temperatures on a horizontal as well as vertical scale. Horizontal spatial variation in air temperatures results from nonuniformity in the surrounding landscape. For instance, a mixture of shrubs, trees and open areas often results in small differences in air temperature of 1–4°C. These differences arise because of differential surface heating (depending on surface spectral and water loss characteristics), and thus result in differences in the rate of sensible heat transfer to upper air layers. On a larger scale, substantial variations in air temperature may arise if two adjacent slopes have different exposures (angles and azimuths). The differential heating in this case would be related to the amount of solar radiation received by that surface (see Sections 7.5 and 7.6).

The point to be made above is that even when air temperatures are measured at a specific height, these values may not be generalizable to a large area. That is, if we are interested in knowing the absolute air temperature at several specific locations, it should be measured at each location if there is reason to believe that spatial heterogeneity in air temperatures exists.

It should be clear from Equation 7.3 above that an accurate estimate of air temperature is critical to being able to predict absolute leaf temperatures. If the variation in air temperatures at a given height is small (say 1–2°C), the absolute air temperature may be measured at a single location and the spatial variation in air temperatures can be overcome by then measuring the differences between leaf and air temperatures at each location. Temperature differentials can be easily measured using thermocouples, and this allows for the precise determinations necessary to evaluate the leaf energy balance equation (see Section 7.4 for a discussion of how to measure leaf/air temperature differentials).

Variation in leaf temperatures exists not only because of differences in air temperatures, but also due to differences in leaf energy balance. For a given air temperature, the maximum range of leaf temperatures (ΔT) can be calculated from Miller (1971) as

$$\Delta T = \frac{a S_d \sin(\alpha) \tan(zn)}{4\,\varepsilon\sigma\,(T_a + 273.15)^3 + h_c + (L)(\mathrm{d}\rho/\mathrm{d}T)/(r_l + r_a)} \tag{7.5}$$

where S_d is the direct component of the solar radiation and zn is the zenith angle, which is equal to 90° minus the solar altitude. Since virtually 100% of all observations occur within eight standard deviations, the standard deviation can be estimated as ΔT divided by 8.

The sample size (n) then required to estimate the mean leaf temperature with a specified confidence interval (c) can be calculated as

$$n = (2ts/c)^2 \tag{7.6}$$

where t is Student's t, usually taken in a first approximation to equal 1.96, and s is the estimated standard deviation in leaf temperatures (Miller, 1971). These equations indicate that in practice to estimate the mean leaf temperature reliably within 0.5°C under high irradiance conditions requires between four and six separate leaf measurements. The required sample size increases to six to ten leaves if a confidence interval of ±0.1°C is necessary. As the solar radiation levels decrease, so does the required sample size for any specified confidence interval. Thus, at low irradiances two to three leaves are usually sufficient to estimate the mean leaf temperature.

7.3.2 Vertical variations in temperature

Vertical gradients in air temperature are well documented (Geiger, 1966; Campbell, 1977; Lee, 1978; Rosenberg *et al.*, 1983). They are associated with surface heating and sensible heat transfer to upper air layers. Steep air temperature gradients of 3–5°C per meter can be established under moderate to dense canopy situations and gradients of 15°C per meter or greater can be established within open arid land communities (Ehleringer, 1985). As a consequence it is critical to measure leaf and air temperatures at equal heights. The magnitude of the error introduced by not measuring leaf and air temperatures at the same height will decrease with increasing height. Thus, a 5 cm difference in sensor placement may result in a 2–5°C error in air temperature estimate near the ground, but only a 0.2–1.0°C error at 1 m.

7.4 TEMPERATURE AND ITS MEASUREMENT

7.4.1 Temperature sensors

In principle there are numerous ways for measuring temperatures of different components within the environment. However, for a variety of reasons most of which will become clear in the following discussion, the commonly practised method for measuring temperatures in physiological ecology is to use thermocouples. Before discussing thermocouples though, it is instructive to present briefly alternative means of temperature measurement and the limitations associated with these approaches.

(a) Bimetallic thermometers

When strips of two different metals having dissimilar expansion coefficients are bonded together, a change in temperature will cause a distortion of the bonded strip. Bimetallic thermometers have bonded bimetallic strips which are shaped into a coil with one end fixed and the other end attached to a needle on a dial. The coiled portion is enclosed within a metal sheath. Temperature changes along the coiled region then cause a rotational motion at the free end. Bimetallic thermometers require that the entire coiled region be in contact with the substance being measured. Thus, they are most useful for measuring solution temperatures. Such sensors are usually very slow in responding, lack the resolution of other temperature measurement devices, and the temperature reading usually must be recorded manually. A common application of bimetallic thermometers is thermographs for recording air temperatures. In this instrument, one end of the metallic strip is attached to a lever at the end of which is an ink pen. Changes in rotational motion in response to temperature change are recorded on a paper trace.

(b) Liquid-in-glass thermometers

In liquid-in-glass thermometers, the liquid (usually mercury) is enclosed within glass in a bulb–capillary arrangement. Temperature is sensed in the bulb region. Thermal expansion of the liquid causes it to rise within the capillary; the calibration is etched on to the glass which encloses the mercury column providing a temperature reading. While inherently more precise than bimetallic thermometers, liquid-in-glass thermometers share many of the same drawbacks as bimetallic thermometers: temperature is measured over a relatively large region, the sensor is slow in responding, and the readout is manual. Liquid-in-glass thermometers are quite precise and are most useful when the temperatures to be measured are uniform over a relatively large distance and a slow response time is acceptable.

(c) Resistance thermometers

Resistance thermometers are perhaps the most precise method for temperature measurement. All metals change electrical resistance with temperature, but metals differ in their temperature coefficient of resistance. Temperature is measured simply by measuring the resistance of a piece of uniform metal. The most common metal used is platinum and the sensor must be enclosed in a casing to protect the metal, which increases the sensor lag time. Unlike the previous two temperature measurement devices, resistance thermometers do not require that the readout device be at the same location as the sensor. Additionally, the resistance can be measured with a meter or automatic data acquisition devices (see Chapter 2). However, since resistance is the parameter being measured, the distance between the sensor and readout device is usually not very long since resistance of the lead wires will add to the total resistance of the circuit. This lead-wire resistance can be compensated for with a four-wire-ohm measurement system, but this adds costs if the distance is long. Mostly because of their relatively large size (when both sensor and casing are included), high expense and relatively slow response time, resistance thermometers are not commonly used temperature-measurement devices within ecology. However, dew-point mirrors used to measure absolute humidities (Chapters 3 and 8) often use resistance thermometers for temperature measurement.

(d) Thermistors

A thermistor is similar to a metal resistance thermometer in that its resistance changes in response to a change in its temperature. Unlike platinum resistance thermometers, thermistors are made of a semiconductor (usually a metallic oxide). Thermistors have greater sensitivity than platinum resistance thermometers (a higher temperature resistance coefficient) and can be made with either positive or negative temperature coefficients, whereas platinum resistance thermometers have only a positive temperature resistance coefficient. Thermistors come in different sizes ranging from small beads (as small as 0.25 mm) to relatively large flat disks. The response time for a temperature change is dependent on thermistor size, and so the smaller sensors can have a relatively fast response. Thermistors can be placed in a different location from their readout device and can be easily incorporated into automated data-acquisition systems. The principal drawbacks to thermistors are that they are more expensive and more fragile than thermocouples, and that in data-acquisition systems, automated resistance reading systems are presently far less common than voltage-measuring systems (as used by thermocouples).

(e) Infrared thermometers

Since all objects at temperatures above 0 K emit radiation, it is possible to measure surface temperatures utilizing this principle. An infrared thermometer senses the amount of longwave radiation emitted by a surface (usually leaf or ground). The intensity of this signal is then converted back to a surface temperature using the Stefan–Boltzmann law of radiation emission: $E = \varepsilon\sigma T_k^4$. The utility of this approach is that the surface need not be touched in order to obtain a temperature reading and that it integrates over a larger surface area. Two drawbacks are that temperatures are usually only accurate to within 0.5°C and that slight differences in emissivity result in large systematic errors in predicted temperature. Additionally, since most hand-held instruments must be focused on the object being measured, it is not practical for experiments involving large numbers of continuous measurements where some degree of automation is required. More sophisticated infrared imaging equipment is available and provides automatic gradient processing not available in hand-held instruments. However, it does so at a much greater cost.

(f) Thermocouples

Thermocouples are small sensors formed by bringing together two dissimilar metals to form a junction. If two dissimilar metallic wires are connected to each other at their ends, a current will flow in this circuit when the two junctions are at different temperatures (Fig. 7.2(a)). The phenomenon was first observed by Johann Seebeck in 1821 and the junction of the two dissimilar metals is called a thermocouple. Both the direction of the current flow and the magnitude of the electromotive force gradient (voltage) produced depend upon the absolute temperature difference between thermocouple junctions J_1 and J_2. The Seebeck effect is the observed conversion of the thermal energy to electrical energy at the thermocouple junction. The Seebeck coefficient is the measure of the voltage gradient produced per unit change in temperature between the two thermocouple junctions. Table 7.4 lists Seebeck coefficients for various kinds of thermocouple junctions.

Table 7.4 Seebeck coefficients for various kinds of thermocouples at 0°C (from *Temperature Measurement Handbook*, Omega Engineering, Stamford, Connecticut)

Type	Metal +	Metal −	Seebeck coefficient ($\mu V\ °C^{-1}$)
E	Chromel	Constantan	58.5
J	Iron	Constantan	50.5
K	Chromel	Alumel	39.4
T	Copper	Constantan	38.7

Shortly thereafter in 1834 James Peltier found that when a current flows across a junction of two dissimilar metals, heat is either given off or absorbed by the junction. The absorption or emission of heat at the junction depends on the direction of current flow and is called the Peltier effect. As more current is applied to the thermocouple junction, there is proportionally more change in its temperature and this is the basis for temperature control in many photosynthetic-measuring systems (Chapter 11). However, with respect to thermocouples as temperature-measuring devices, there is no measurable change in the temperature of a thermocouple when the current flowing across it is due solely to the thermal electromotive force.

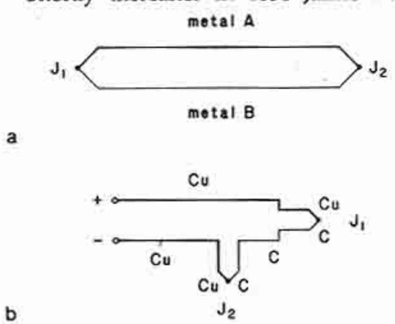

Fig. 7.2 (a) Seebeck effect – current will flow as long as two junctions are at different temperatures. (b) A system for temperature measurement using two thermocouple junctions (one for measuring and the other as reference) where J_1 is the sensing thermocouple and J_2 is the reference thermocouple and Cu and C indicate copper and constantan wire respectively.

In 1851 William Thompson found that current flowing through a single homogeneous conductor will liberate or absorb heat if a temperature gradient exists within that conductor. The Thompson effect occurs both within wires to which a current has been applied as well as to those generated by thermocouples. The thermoelectric electromotive force (Seebeck effect) is then the sum of the Peltier electromotive forces at the junctions and the Thompson electromotive forces in the two different wires.

Thermocouples are inexpensive, come in various sizes and respond relatively fast to a change in temperature. An additional feature which makes thermocouples quite popular is that the distance between the sensor and the readout device can be variable and long without affecting the signal. The measurement signal is a voltage and the sensors are

easily incorporated into data-acquisition systems. Their principal drawback was that before the availability of operational amplifiers the signal voltage was low and more difficult to resolve. That problem has been easily overcome with today's accurate and more powerful voltage amplification systems.

For most applications, we are interested in knowing the absolute temperature of one of the thermocouple junctions. In these situations the temperature of the other thermocouple junction (called the reference junction) must be known and the voltage gradient within the circuit is then measured with a voltmeter. The reference junction is most commonly at 0°C, and this is achieved by either placing the reference junction into a container (usually a thermos or Dewar flask) of ice water or utilizing an electronic compensation circuit (most common approach) which achieves the same effect. Fig. 7.2(b) illustrates a typical copper–constantan thermocouple setup where J_1 is the measuring thermocouple junction and J_2 is the reference junction; in this setup, the voltage is measured by a voltmeter across the positive/negative leads.

Copper–constantan thermocouples are the most commonly used in environmental sciences (Table 7.4). The Seebeck coefficient for this combination of two different metals is relatively high, ranging from 38.7 $\mu V\ °C^{-1}$ at 0°C to 46.8 $\mu V\ °C^{-1}$ at 100°C. The use of copper as a junction minimizes potential additional thermocouple effects when leads are connected to a measuring device. Thermocouples may be commercially purchased, but they are also easily constructed from paired thermocouple wire. The thermocouple junction is the sensing element for temperature. It may be constructed by twisting the two different wires together (in which case it is the first junction of the twist which becomes the measurement location), and then binding them together with solder (no effect on temperature measurement), or by butt-welding the two wires.

Thermocouples have the added advantage that the wire is relatively inexpensive and that it is very uniform in composition. The uniformity means that there will be little variation between different thermocouples, and thus they do not have to be individually calibrated. However, there are some minor disadvantages to thermocouples, especially to those in which copper forms one of the junctions. The disadvantages are that copper has a high thermal conductivity so that heat conduction to the thermocouple junction could be a problem (especially at low wind speeds when the wire is in full sun) and that, in the smaller gauges, copper is not very stiff and therefore thermocouple penetration of a surface (such as a leaf epidermis) might be difficult.

Thermocouples can be arranged together for two very different applications. When closely linked together in series, they provide a larger signal output (roughly equivalent to the product of the Seebeck coefficient and the number of thermocouple junctions). Many thermocouple junctions in series are called a thermopile and this is the basis of many pyranometers (see Chapter 6). Alternatively, when thermocouples are arranged in parallel, they then estimate the average temperature. One common application is to measure the average leaf temperature by placing three to five thermocouples in a parallel arrangement. The obvious advantage is that only one junction to a data-acquisition device is needed to get the average temperature reading, saving two to four input channels for additional kinds of measurements.

Thermocouple wire comes in various diameters (Table 7.5). Two of the more commonly used gauges are 36 AWG for leaves and other thin objects and 24 AWG for air and soil temperatures.

When given a step change in the temperature of the object being measured, thermocouples and other sensors respond in an exponential manner. Thermocouples respond relatively fast to changes in temperature. The time constant, which is the time

Table 7.5 Wire gauge and diameter

AWG*	Diameter (mm)
16	1.29
24	0.51
36	0.13
40	0.08
44	0.05

* AWG = American wire gauge.

required for the sensor to complete 1/e of the step change in temperature, is a function of wire diameter. For 16 AWG wire, the time constant is 3.1 s, which means that approximately 14.3 s are required for the thermocouple to go 99% of the step change in temperature. The time constant decreases with wire diameter; for 24 AWG wire, the time constant is 0.9 s, and for 36 AWG wire it is 0.09 s.

While long time constants may not be useful if you wish to know the temperature of an object that is changing rapidly, there are occasionally applications in which an averaged temperature is preferred. In such situations, thermocouples with longer time constants are desired because they will better integrate the 'running average' temperature.

7.4.2 Thermocouple sensor errors

(a) Thermocouple size

Choosing the appropriate thermocouple size for the object to be measured is quite important. The mass of the thermocouple should be small relative to the object being measured (such as a leaf), otherwise the sensor unduly influences the temperature of the object. Thus, a 36 or 40 AWG thermocouple is appropriate for most thin leaves, but a 24 AWG is much too large as its mass and diameter are of similar magnitude to that of the leaf thickness. Virtually any gauge is appropriate for sensing air and/or soil temperatures. The ultimate choice will depend on the time constant appropriate for the object being measured.

The same thermocouple gauge need not be maintained all the way from the measuring junction to the measurement device. It is common to use a 36 AWG thermocouple of 50 cm total length to measure leaf temperature and then to use a 24 AWG wire (which is more rugged) to continue on to the meter or data-acquisition device. When this is done, it is essential to use thermocouple connectors which maintain copper and constantan continuity within the line.

(b) Attachment to leaf

Ideally, thermocouples should be inserted into the center of the leaf mesophyll tissues from the underside. This should be done with a minimum of disruption to the epidermal layer to avoid causing excessive transpirational changes. The thermocouple should be attached in such a way that it does not change the leaf orientation (angle and azimuth). Some investigators have found that thermocouples can be attached to the lower leaf surface using surgical tape with no errors in the measurement.

Vertical leaf temperature gradients do not occur in leaves (Hays, 1975), but large temperature gradients can develop across leaves depending on the magnitude of the leaf boundary layer (Drake *et al.*, 1970; Wiebe and Drake, 1980). Thus, for large leaves or in low wind speed and high irradiance environments, several thermocouples are necessary to estimate accurately the average leaf temperature (Miller, 1971).

(c) Radiation errors

It is assumed that the thermocouple is in equilibrium with the object whose temperature it is measuring, but this will not necessarily be the case if the thermocouple is exposed to solar radiation. Solar radiation loads incident on a thermocouple will cause

its temperature to increase and thus deviate from the temperature of the object. The extent of the deviation can be predicted by the energy budget equation, since thermocouple temperatures are subject to the same constraints as any other object.

Consider a thermocouple which has been placed on top of a leaf to measure the leaf temperature. If the thermocouple is at the true temperature, then the second term of Equation 7.3 will be zero. The error in the thermocouple temperature reading will be a function of the total solar radiation load, wind speed at the leaf surface (usually close to zero), and thermocouple size. The largest of these error components will be the solar radiation load. Under extreme conditions, the error in leaf temperature measurement caused by exposing a leaf thermocouple to direct sunlight can approach several degrees. To reduce this error, thermocouples should be inserted into the lower surface tissue.

This same type of error can appear in air and soil surface temperature measurements. For soil surface temperature measurements, the thermocouple should be inserted several millimeters below the surface to minimize potential radiation errors, yet allowing for reliable soil surface temperature estimates. For air temperature measurements, the thermocouple should be shielded from solar radiation yet should receive full wind exposure. This is normally accomplished using two flat plates to sandwich the thermocouple, each painted white on their outer surfaces and black on their inner surfaces. These plates are placed several centimeters above and below the thermocouple to allow for adequate ventilation (Fig. 7.3).

Leaf minus air temperature differentials can be most accurately measured by using the air temperature as the reference junction instead of an ice point reference. In this way the absolute leaf temperature is not measured, but instead the difference between temperature of the air and leaf is directly sensed. This allows for the air temperature to be measured near the leaf avoiding potential spatial variation errors. It also provides a more accurate estimate of the true temperature differential, since the differential is measured directly rather than calculating it from two absolute values. When temperature differentials are measured, an additional absolute and independent reading of either air or leaf temperature is required in order to obtain absolute estimates for each reading.

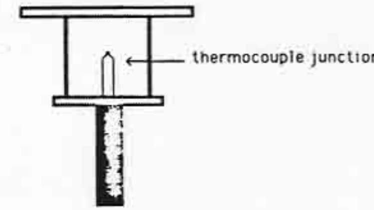

Fig. 7.3 An air temperature shield to reduce radiation error on the thermocouple.

7.4.3 Time constants

When measuring temperatures of various components within the environment, it is important to make sure that the thermocouple sensor is able to track adequately and rapidly the changes in temperature of the object being measured. In the previous section, we mentioned that time constants, the time required to complete 1/e (37%) of the step change, varied from 0.9 s for 24 AWG to 0.09 s for 36 AWG thermocouples. For most studies in physiological ecology these time constants are more than sufficient to track changes in air, soil and tissue temperatures. The time constant of a single exposed leaf or a leaf within a canopy to a change in solar radiation is approximately 10 s, and complete equilibration usually occurs within 40–60 s (Wiegand and Swanson, 1973). Soils respond somewhat slower and the time constant for the soil surface was estimated to be approximately 100 s by Wiegand and Swanson (1973).

7.5 ORIENTATION AND ITS MEASUREMENT

The orientation of a leaf or any other surface is important for understanding the diurnal and seasonal patterns of solar radiation incident on that surface. For leaves, these solar radiation intensities will significantly influence both photosynthetic rate (via its effect on the 400–700 nm photon flux) and leaf temperature (via its effect on total solar radiation). For ground surfaces, the amount of solar radiation will influence the heating of the surface, and therefore greatly affect soil and air temperature profiles. The amount of solar radiation that is incident on a leaf or ground surface can be specified for clear sky conditions if the direct and diffuse components of solar radiation incident on a horizontal surface and the leaf angle and its azimuth are known.

7.5.1 Cosine of angle of incidence

The cosine of the angle of incidence ($\cos(i)$) is a measure of the fraction of the direct solar radiation beam that is striking a planar surface. It varies between 0 and 1 depending on the relative geometrical positions of the surface and sun. We can describe $\cos(i)$ as

$$\cos(i) = \cos(\alpha_1)\sin(\alpha_s) + \sin(\alpha_l)\cos(\alpha_s)\cos(\beta_s - \beta_l) \quad (7.7)$$

where α_l and α_s are the angles above the horizon of the surface (e.g. leaf) and sun and β_l and β_s are the azimuthal positions of the surface and sun respectively (Gates, 1962).

7.5.2 Angle

The leaf angle (sometimes referred to as the leaf inclination) and solar angle (sometimes referred to as the solar altitude or elevation) are measured from the horizontal. Thus, a horizontal leaf has a leaf angle of 0° and when the sun is directly overhead (which never occurs if the latitude is greater than 23.5°), its solar angle is 90°.

Angles are often measured using an inclinometer, a small portable device that allows precise rapid angle determinations. Alternatively, leaf and solar angles can be measured with a protractor and plumb line.

In canopies with high leaf area indices, leaf angles often vary with canopy position, and so caution should be exercised to avoid introducing an unwanted variable by neglecting canopy position. It should also be noted that in some plants leaf angles are known to change seasonally in response to water stress (Comstock and Mahall, 1985) and in other plants leaves will move diurnally (Ehleringer and Forseth, 1980). In those leaves with diurnal movements, the leaves usually move so that they face the sun ($\cos(i) = 1.0$) throughout the day.

7.5.3 Azimuth

The azimuth represents the compass direction. It is measured with a compass (remember that a magnetic deviation must be incorporated to give the true azimuthal direction). Azimuths are recorded with respect to due south, thus south has a value of 0°, east −90°, west +90°, and north ±180°. The azimuth of the sun is relatively easy to determine when solar angles are low, but is more difficult to measure when the sun is at angles above 70°. This potential problem can be overcome by using a vertical piece of paper above the compass and orienting the compass until there is no shadow cast by the paper. For leaves, the direction that a leaf blade faces is again determined using a compass, but this direction is not necessarily the same as the petiolar–blade axis. The leaf azimuth is the direction that water would roll off a planar leaf surface.

7.6 CALCULATION OF INCIDENT SOLAR RADIATION ON DIFFERENT SURFACES

The effects of changes in latitude, season and

slope characteristics can have a pronounced impact on the intensity of solar radiation received by a surface. The diurnal changes in the intensity of solar radiation incident on any surface (leaf, ground, etc.) with a specified slope and azimuth at any latitude and at any time of the year can be reliably predicted for clear sky conditions given several parameters.

Under clear sky conditions, the intensity of solar radiation on any surface can be calculated knowing the altitude and azimuth of the sun and angle and azimuth of the surface of interest. The solar altitude (angle above the horizon) is

$$\sin(\alpha_s) = \sin(l)\sin(D) + \cos(l)\cos(D)\cos(h) \quad (7.8)$$

where α_s is the solar altitude, l is the latitude, D is the solar declination and h is the solar hour angle (List, 1968). The hour angle equals

$$h = (t-12)(\pi/12) \quad (7.9)$$

where t is the mean solar time in hours.

The azimuth of the sun (β_s) can be described as

$$\beta_s = -\arcsin[-\cos(D)\sin(h)/\cos(\alpha_s)] \quad (7.10)$$

The declination varies from −23.5° to +23.5° depending on the time of the year. In the northern hemisphere, the declination can be described by

$$D = 23.5\cos[2\pi(d-172)/365] \quad (7.11)$$

where d is the day of the year (Rosenberg *et al.*, 1983).

Equations 7.8 and 7.10 allow the path of the sun through the sky to be calculated for different locations and seasons.

Once these values are known, we can calculate the irradiance incident on a horizontal plane at the earth's surface as

$$I_o = S_c\sin(\alpha_a)A^{[l/\sin)\alpha_s)]} \quad (7.12)$$

where I_o is the irradiance incident on a horizontal surface, S_c is the solar constant and A is the atmospheric transmission coefficient. The solar constant has a value of 1350 W m^{-2} for the 400–3000 nm waveband and for photosynthetically useful wavelengths (400–700 nm) its value is 2.79 mmol m^{-2} s^{-1}. The atmospheric transmission coefficient is a function of air clarity and the thickness of the air column (which varies diurnally). Under clear skies at sea level, the atmospheric transmission coefficient is approximately 0.8. At higher elevations, it increases to approximately 0.85. Under light haze conditions, the atmospheric transmission coefficient decreases to 0.5–0.6.

For slopes with inclinations other than horizontal and with different azimuths, the intensity of solar radiation incident on those slopes (I_s) becomes

$$I_s = I_o\cos(i)/\sin(\alpha_s) \quad (7.13)$$

7.7 LEAF ABSORPTANCE AND ITS MEASUREMENT

Light is absorbed by, reflected from or transmitted through, a surface. The sum of these three fractional components is one. For leaves and other biological materials, we are often most interested in knowing what fraction of the radiation is absorbed. In the past these measurements have often been obtained by measuring leaf surface reflectance properties and assuming that transmittance through the leaf is neglible. This is incorrect and can lead to overestimates in leaf absorptance values since leaf transmittance between 400 and 700 nm can vary by 2–12% between species (Moss and Loomis, 1952).

Leaf absorptance is a measurement of the fraction of the incident photon or energy flux that is absorbed by the leaf. It can be measured at a single wavelength or over a specific waveband. When leaf absorptances are expressed for a particular waveband (such as between 400 and 700 nm), the irradiance source (such as sunlight) must be specified. Over the visible wavelengths (400–700 nm), the leaf absorptance to sunlight on either a photon or energy flux basis is nearly identical and is frequently used interchangeably (Ehleringer and Björkman, 1978; Gates, 1980). Leaf absorptances between 400 and 700 nm mentioned in this chapter have been measured on a photon basis unless otherwise noted. This is because of the rapidity and ease with which the leaf photon absorptance can be measured.

7.7.1 Measurement of leaf absorptances

Leaf absorptances (a) are measured with an integrating sphere. There are two basic types: the Ulbricht sphere (Rabideau *et al.*, 1946), in which the leaf sample is positioned inside the sphere during measurement (Fig. 7.4), and the Taylor sphere (Taylor, 1920), in which the sample is positioned at a port on the outside surface of the sphere during the measurement. A significant attribute of the Ulbricht sphere for leaf absorptance measurements is that only a single measurement needs to be made to obtain leaf absorptance. In an Ulbricht sphere, light enters the integrating sphere and strikes the leaf sample, which is suspended in the center of the sphere interior. All light not absorbed is either reflected off the leaf surface or is transmitted through the leaf. The inside walls of the integrating sphere are coated with magnesium oxide powder, which has the unusual property that its absolute reflectance is 0.99 at all wavelengths between 350 and 2000 nm (Kortüm, 1969). Occasionally, barium sulfate, which has an absolute reflectance of 0.90–0.95 between 350 and 2000 nm, is substituted for magnesium oxide (Kortüm, 1969). The intensity of the photon flux reflecting off the sphere walls, when the leaf is in the path of the incoming beam (I_{in}), is measured with either a silicon cell or a LI-COR Quantum Sensor. This value is then compared with the photon flux resulting when the sample has been pulled out of the beam (I_{out}). With the leaf out of the sample beam, light instead strikes a magnesium oxide reflectance standard. The leaf absorptance is then calculated as

$$a = 1 - I_{in}/I_{out} \qquad (7.14)$$

In contrast, the Taylor integrating sphere requires two separate measurements. In the first measurement, light passes through the

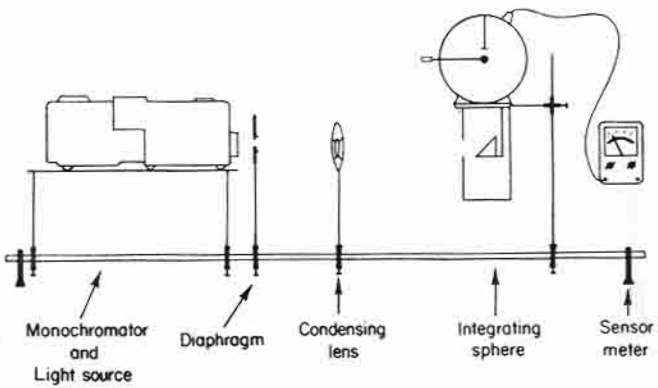

Fig. 7.4 Ulbricht integrating sphere (from Ehleringer, 1981).

sphere and strikes either the leaf sample or a reflectance standard. Light reflected back into the sphere is measured by a sensor and reflectance is then calculated as the ratio of the signal when light strikes the leaf to that when it reflects from the reference. To estimate transmittance the leaf is placed at the point where light would normally enter the sphere. The transmittance is then the ratio of the signal when the leaf is in the opening to when it is removed from the opening. The leaf absorptance is then calculated as one minus the reflectance minus the transmittance.

7.7.2 Visible versus total solar absorptance

Leaf absorptance to visible wavelengths (400–700 nm) is useful for understanding the fraction of incident photons that can be used in photosynthesis; these values are generally about 85% in most mature green leaves (Gates *et al.*, 1965; Gates, 1980; Ehleringer, 1981). In contrast, there is much less absorption of wavelengths beyond 700 nm, even though almost one half of the solar radiation at the earth's surface is in wavelengths between 700 and 3000 nm. Most of the solar radiation absorbed beyond 700 nm is due to five broad water absorption bands distributed between 900 and 3000 nm; only a small fraction of the solar radiation is absorbed by pigments such as phytochrome. As a consequence the leaf absorptance to solar radiation (400–3000 nm) is generally about 50%.

The integrated leaf absorptance to sunlight between 400 and 700 nm can be measured by integrating the leaf absorptance spectrum with the solar radiation spectrum or it can be more easily measured by using sunlight as a light source into the integrating sphere and using a LI-COR Quantum Sensor (which measures only 400–700 nm photons) to determine absorptance. An even simpler approach was found by Ehleringer (1981), where it was shown that the leaf absorptance at 625 nm was equal to the integrated leaf absorptance to sunlight between 400 and 700 nm. This held true for a wide diversity of plant species with leaf absorptances ranging from 30 to 90%.

While the leaf absorptances to 400–700 nm are useful for photosynthetic studies, the leaf absorptance to total solar radiation is most useful for heat and energy balance studies. These two leaf absorptances are expected to be closely linked since leaves absorb primarily in the visible wavelengths. Ehleringer (1981) found from sampling different leaves over a large range of absorptances that the leaf absorptance to total solar radiation (%) was related to the visible waveband absorptance as

$$a_{400-3000} = 0.73a_{400-700} - 11.9 \qquad (7.15)$$

7.7.3 Leaf absorptance data

The leaf absorptance will depend primarily on the epidermal characteristics and on leaf chlorophyll content. Except for developing and senescing leaves, it appears that leaf chlorophyll contents are sufficiently high that changes in leaf absorptance are largely due to

Table 7.6 Estimates of leaf absorptance to solar radiation by different species for the 400–700 nm waveband (useful for photosynthetic studies) and the 400–3000 nm waveband (useful for energy budget and heat balance studies). Data are from Birkebak and Birkebak (1964) and Ehleringer (1981, 1988).

Species	$a_{400-700}$	$a_{400-3000}$
Acer negundo	0.80	0.50
Acer saccharinum	–	0.49
Atriplex hymenelytra	0.66	0.39
Encelia farinosa	0.42	0.21
	0.63	0.35
	0.81	0.49
Fraxinus pennsylvanica	–	0.50
Geraea canescens	0.81	0.48
Malvastrum rotundifolium	0.83	0.46
Populus tremuloides	0.86	0.49
Quercus alba	–	0.49
Quercus rubra	–	0.49

variations in epidermal properties (Lin and Ehleringer, 1982, 1983). Table 7.6 lists leaf absorptances to sunlight for the 400–700 nm and 400–3000 nm wavebands for a number of species from diverse habitats. The differences in leaf absorptance are principally due to epidermal modifications such as pubescence and waxes.

7.8 BOUNDARY LAYER CONSIDERATIONS

Wind and its effects on leaf boundary layers have been discussed in Chapter 4. Suffice it to reiterate here that both wind speed and leaf size and shape will influence the magnitude of the leaf boundary layer and the resistances to heat and water vapor transfer across this layer of laminar air flow. The reader is referred to Chapter 4 for a complete description of wind and boundary layers and for values of the convection coefficients as a function of leaf size and shape.

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