

# 16 Leaf energy fluxes

## 16.1 Chapter summary

Individual leaves in the plant canopy absorb radiation and exchange sensible heat and latent heat with the surrounding air. Sensible heat flux and latent heat flux are important biophysical processes that govern leaf temperature. The efficient transfer away from the leaf surface of heat during convection and moisture during transpiration cools the leaf. These fluxes are regulated in part by leaf boundary layer resistance and stomatal resistance. Large resistances decrease fluxes, all other factors being equal. The size and shape of leaves govern leaf boundary layer resistance, as well as the depth of the boundary layer over the leaf surface. A thin boundary layer, which is typical of small or deeply lobed leaves, allows strong coupling between the leaf surface and the surrounding air (low resistance). Larger or less lobed leaves typically have a thicker boundary layer and are more decoupled from the surrounding air (high resistance). As a result, the size and shape of leaves are closely matched to environment. Large leaves are favored in warm to hot climates with low light levels. Small leaves are favored in sunny environments and in cold climates.

## 16.2 Leaf energy budget

For a leaf, net radiation ( $R_n$ ) is balanced by sensible heat ( $H$ ) and latent heat ( $\lambda E$ ):

$$R_n = H + \lambda E \quad (16.1)$$

so that, from equation (13.13):

$$Q_a = \epsilon \sigma (T_s + 273.15)^4 + \rho C_p \frac{(T_s - T_a)}{r_H} + \frac{\rho C_p (e_s [T_s] - e_a)}{\gamma r_W} \quad (16.2)$$

In (16.2),  $Q_a$  is the radiative forcing, defined as the sum of absorbed solar radiation and incident longwave radiation. Longwave radiation is emitted by the leaf in proportion to

its temperature ( $T_s$ , °C) raised to the fourth power. Sensible heat is exchanged between the leaf and surrounding air ( $T_a$ , °C) in proportion to the temperature difference divided by a diffusion resistance ( $r_H$ , s m<sup>-1</sup>). Similarly, latent heat is exchanged in relation to the vapor pressure deficit between the leaf, assumed to be saturated with moisture ( $e_s [T_s]$ , Pa), and the surrounding air ( $e_a$ , Pa) divided by a diffusion resistance ( $r_W$ , s m<sup>-1</sup>).

## 16.3 Leaf resistances

The fluxes of sensible heat, latent heat, and CO<sub>2</sub> from a leaf can be represented as a diffusion process analogous to electrical networks (Fig. 16.1). The electrical current between two points on a conducting wire is equal to the voltage difference divided by the electrical resistance. For an electrical circuit with two resistors connected in series, the total resistance is the sum of the individual resistances. Similarly, the diffusion of materials is related to the concentration difference divided by a resistance to diffusion. For sensible heat, this diffusion resistance is defined by the leaf boundary layer resistance. The exchanges of water vapor and CO<sub>2</sub> between a leaf and the surrounding air depend on two resistances connected in series: a stomatal resistance from inside the leaf to the leaf surface and a boundary layer resistance from the leaf surface to the air. If stomata are located on both sides of the leaf, the upper and lower resistances acting in parallel determine the overall leaf resistance.

The boundary layer resistance ( $r_b$ ) governs heat and moisture exchange between the leaf surface and the air around the leaf. This resistance depends on leaf size

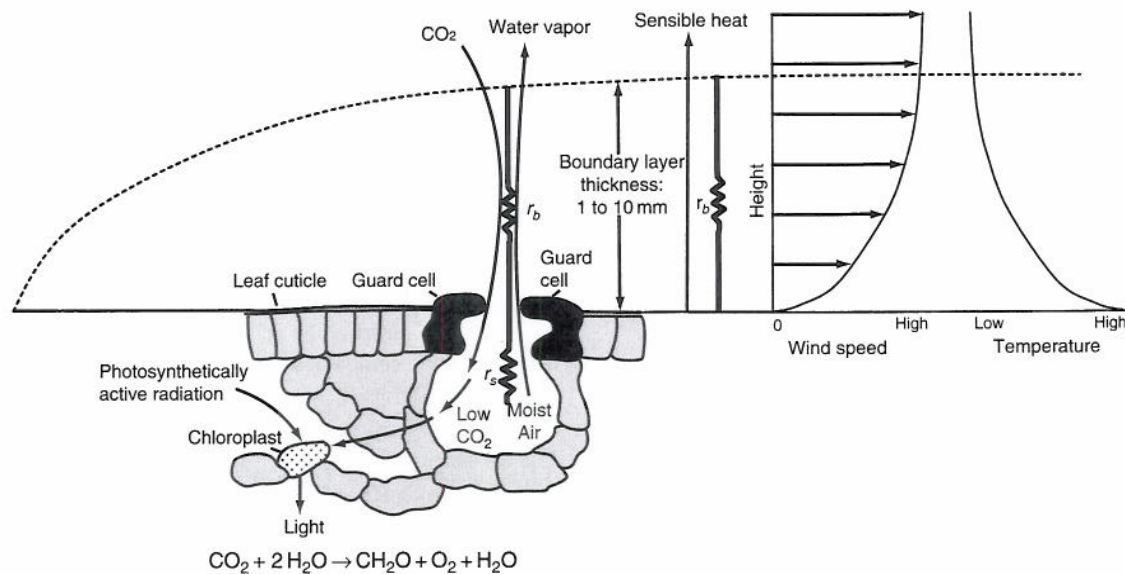
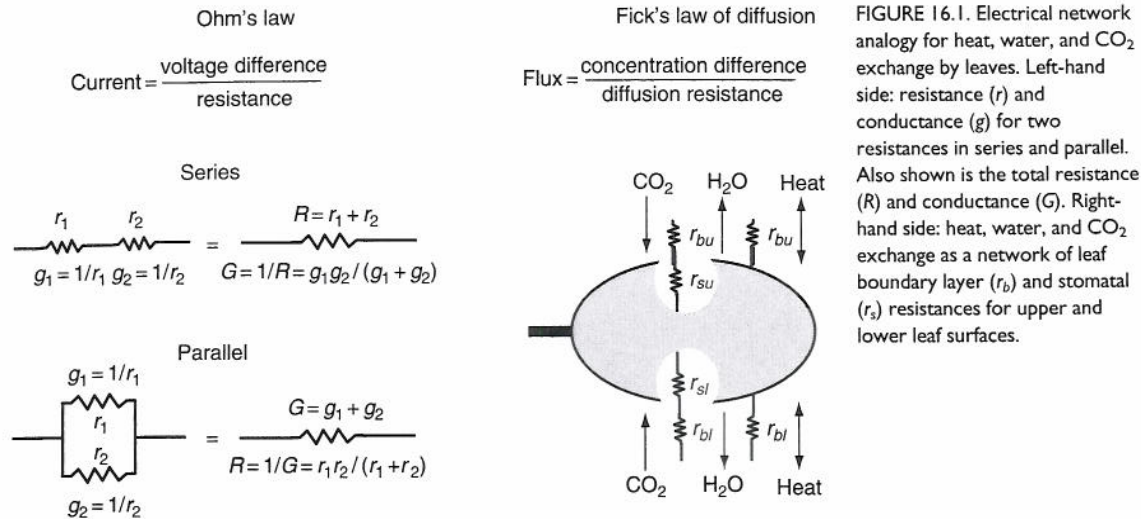


FIGURE 16.2. Leaf boundary layer processes. Shown are stomata and associated  $\text{CO}_2$  and water fluxes. These fluxes are regulated by stomatal ( $r_s$ ) and boundary layer ( $r_b$ ) resistances. Also shown are boundary layer thickness and associated wind and temperature profiles. Sensible heat flux is regulated by  $r_b$ .

( $d$ , m) and wind speed ( $u$ ,  $\text{m s}^{-1}$ ) and is approximated per unit leaf area (one-sided) as

$$r_b = 200\sqrt{d/u} \quad (16.3)$$

This resistance has units of seconds per meter ( $\text{s m}^{-1}$ ). Plant physiologists often use  $\text{m}^2 \text{s mol}^{-1}$  instead of  $\text{s m}^{-1}$ . At sea level and  $20^\circ\text{C}$ ,  $1 \text{ m}^2 \text{s mol}^{-1} = 41 \text{ s m}^{-1}$  (Jones 1992, p. 357).

The boundary layer resistance represents the resistance to heat and moisture transfer between the leaf surface and free air above the leaf surface. Wind flowing across a leaf is slowed near the leaf surface and increases with distance from the surface (Fig. 16.2). Full wind flow occurs only at some distance from the leaf surface. This transition zone, in which wind speed increases with distance from the surface, is



known as the leaf boundary layer. It is typically 1–10 mm thick. The boundary layer is also a region of temperature and moisture transition from a typically hot, moist leaf surface to cooler, drier air away from the surface. The boundary layer regulates heat and moisture exchange between a leaf and the air. A thin boundary layer produces a small resistance to heat and moisture transfer. The leaf is closely coupled to the air and has a temperature similar to that of air. A thick boundary layer produces a large resistance to heat and moisture transfer. Conditions at the leaf surface are decoupled from the surrounding air and the leaf is several degrees warmer than air.

This expression for boundary layer resistance is derived for a fluid moving smoothly across a surface – a condition known as laminar forced convection (Gates 1980; Monteith and Unsworth 1990; Campbell and Norman 1998). For a flat plate of length  $d$  (m), the resistance to heat transfer from one side of the plate is

$$r_b = (\rho C_p d) / (k \text{Nu}) \quad (16.4)$$

where  $\rho$  is the density of the fluid ( $\text{kg m}^{-3}$ ),  $C_p$  is the specific heat of the fluid ( $\text{J kg}^{-1} \text{ }^\circ\text{C}^{-1}$ ),  $k$  is the thermal conductivity of the fluid ( $\text{W m}^{-1} \text{ }^\circ\text{C}^{-1}$ ), and Nu is the dimensionless Nusselt number. For a flat plate with laminar flow:

$$\text{Nu} = 0.66 \text{Re}^{0.5} \text{Pr}^{0.33} \quad (16.5)$$

where Pr is the dimensionless Prandtl number and Re is the dimensionless Reynolds number. The Reynolds number depends on fluid velocity ( $u$ ,  $\text{m s}^{-1}$ ) and kinematic viscosity ( $\nu$ ,  $\text{m}^2 \text{s}^{-1}$ ):

$$\text{Re} = ud/\nu \quad (16.6)$$

Combining (16.4), (16.5), and (16.6):

$$r_b = \left( \frac{\rho C_p \sqrt{\nu}}{0.66k \text{Pr}^{0.33}} \right) \sqrt{d/u} = a\sqrt{d/u} \quad (16.7)$$

For air at  $20^\circ\text{C}$ ,  $\rho = 1.204 \text{ kg m}^{-3}$ ,  $C_p = 1010 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$ ,  $\nu = 15.5 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ ,  $k = 0.026 \text{ W m}^{-1} \text{ }^\circ\text{C}^{-1}$ , and  $\text{Pr} = 0.72$  so that  $a = 312 \text{ s}^{1/2} \text{ m}^{-1}$  for a flat plate. Values of Nu for leaves are generally higher, so that  $r_b$  is lower, than that of a flat plate. The boundary layer resistance for flat plates must be divided by 1.4 for leaves in the field (Campbell and Norman 1998, p. 224), which gives  $a = 223 \text{ s}^{1/2} \text{ m}^{-1}$ . Gates (1980, pp. 297–303) recommended a value of  $174 \text{ s}^{1/2} \text{ m}^{-1}$  for leaves. An approximate value for leaves is  $a = 200 \text{ s}^{1/2} \text{ m}^{-1}$ . This is the resistance for heat exchange from one side of a leaf. Sensible heat is exchanged from both sides of a leaf so that heat exchange is regulated by two resistances (each defined by  $r_b$ ) in parallel (Fig. 16.1) and the effective resistance for heat transfer is  $r_H = r_b/2$ . Campbell (1977, pp. 119–123) also noted that  $r_b$  must be

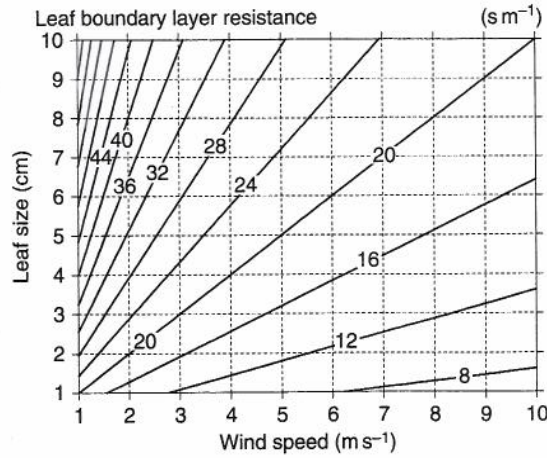


FIGURE 16.3. Leaf boundary layer resistance  $r_b$  (16.3) in relation to leaf size and wind speed.

reduced by one-half for sensible heat, and Jones (1992, p. 63) distinguished between one-sided and two-sided heat transfer. This resistance increases with leaf size and decreases with wind speed (Fig. 16.3).

Stomatal resistance ( $r_s$ ) acts in series with boundary layer resistance to regulate transpiration. Transpiration occurs when stomata open to allow a leaf to absorb  $\text{CO}_2$  during photosynthesis (Fig. 16.2). At the same time, water diffuses out of the saturated cavities within the foliage to the drier air surrounding the leaf. The resistance for latent heat exchange, therefore, includes two terms: a stomatal resistance ( $r_s$ ), which governs the flow of water from inside the leaf to the leaf surface, and the boundary layer resistance, which governs the flow of water from the leaf surface to surrounding air. The total resistance is the sum of these two resistances ( $r_W = r_s + r_b$ ). Stomata open and close in response to a variety of conditions (Chapter 17): they open with higher light levels; they close with temperatures colder or hotter than some optimum; they close as the soil dries; they close if the surrounding air is too dry; and they vary with atmospheric  $\text{CO}_2$  concentration. Stomatal resistance is a measure of how open the pores are and varies from about  $100 \text{ s m}^{-1}$  when stomata are open to greater than  $5000 \text{ s m}^{-1}$  when stomata are closed. For transpiration, the boundary layer resistance, which is formulated based on heat exchange from one side of a leaf, is not reduced by one-half because stomata are typically, but not always, located on one side of a leaf whereas sensible heat exchange occurs on both sides. For example, Gates (1980, p. 27, p. 30, p. 32, p. 351) used  $a = 133 \text{ s}^{1/2} \text{ m}^{-1}$  for sensible heat and  $a = 200 \text{ s}^{1/2} \text{ m}^{-1}$  for latent heat. Campbell (1977, pp. 119–123) reduced  $r_b$  by one-half for sensible heat but not latent heat when stomata are on one side of the leaf. If stomata are on both sides of the leaf, the resistances are in parallel (Fig. 16.1).



TABLE 16.1. Surface temperature for radiative forcing of 1000, 700, and 400 W m<sup>-2</sup> with (a) longwave radiation only ( $L\uparrow$ ), (b) longwave radiation and convection ( $L\uparrow + H$ ), and (c) longwave radiation, convection, and transpiration ( $L\uparrow + H + \lambda E$ )

$Q_a$ (W m <sup>-2</sup> )	Temperature (°C)						
	$L\uparrow + H$				$L\uparrow + H + \lambda E$		
	$L\uparrow$	0.1 m s <sup>-1</sup>	0.9 m s <sup>-1</sup>	4.5 m s <sup>-1</sup>	0.1 m s <sup>-1</sup>	0.9 m s <sup>-1</sup>	4.5 m s <sup>-1</sup>
1000	91	53	39	34	39	33	31
700	60	40	34	32	32	29	29
400	17	26	28	29	23	26	27

Note. Leaf temperature is calculated from (16.2). Air temperature is 29 °C, relative humidity is 50%, and wind speeds are 0.1, 0.9, and 4.5 m s<sup>-1</sup>. Stomatal resistance is 100 s m<sup>-1</sup> and leaf dimension is 5 cm. In this example,  $\rho = 1.15$  kg m<sup>-3</sup>,  $C_p = 1005$  J kg<sup>-1</sup> °C<sup>-1</sup>,  $\gamma = 66.5$  Pa °C<sup>-1</sup>, and  $\epsilon = 1$ .

## 16.4 Leaf fluxes and temperature

Leaf temperature is the temperature that balances the leaf energy budget (16.2). Analysis of the energy budget and the resulting leaf temperature under a variety of environmental conditions gives important insight to the leaf microclimate. For example, Table 16.1 shows the importance of sensible and latent heat in reducing leaf temperature under a variety of radiative forcings and wind speeds for a summer day. The leaf has a radiative forcing of 1000, 700, and 400 W m<sup>-2</sup>, which is representative of values for a clear sky at midday, a cloudy sky at midday, and night, when solar radiation is zero and the leaf receives only longwave radiation. If longwave radiation is the only means to dissipate this energy, the leaf has temperatures of 91, 60, and 17 °C with high, moderate, and low radiative forcings, respectively.

Heat loss by convection (i.e., sensible heat) cools the leaf (Table 16.1). Under calm conditions, with a wind speed of 0.1 m s<sup>-1</sup>, sensible heat loss decreases leaf temperature by 38 °C (to a temperature of 53 °C) with the high radiative forcing and by 20 °C (to a temperature of 40 °C) with the moderate forcing. Higher wind speeds lead to even lower temperatures. At 4.5 m s<sup>-1</sup>, the temperature of the leaf exposed to the high radiative forcing has been reduced from 91 to 34 °C. At low radiative forcing, convection warms the leaf because it is colder than the surrounding air and heat is transferred from the air to the leaf. This example illustrates the powerful effect wind has in transporting heat away from an object, thereby cooling the object.

Latent heat exchange also decreases leaf temperature (Table 16.1). Under calm conditions (0.1 m s<sup>-1</sup>) and high radiative forcing, transpiration decreases leaf temperature by an additional 14 °C, from a temperature of 53 °C with longwave radiation and convection to a temperature of 39 °C. Higher winds result in even lower temperatures. With a wind speed of 4.5 m s<sup>-1</sup>, the leaf temperature has been reduced from a lethal temperature of 91 °C with longwave

radiation only to a more comfortable temperature of 31 °C. Cooling by transpiration is greatest with large radiative forcing and decreases as radiation decreases. It is largest for calm conditions and decreases as wind increases.

Figure 16.4 shows the cooling effect of transpiration in more detail over a range of air temperature and relative humidity. Latent heat flux decreases and leaf temperature increases as relative humidity increases. For example, with an air temperature of 30 °C and a relative humidity of 10%, the leaf temperature is 27.5 °C. This is 2.5 °C colder than the air. At 55% relative humidity, leaf temperature is approximately equal to air temperature, and leaf temperature is more than 2 °C warmer than air temperature at 90% relative humidity. The same is true for all air temperatures: transpiration cooling decreases and leaf temperature increases as relative humidity increases. For air temperature greater than 21 °C, the relative humidity at which the leaf is warmer than air increases as air temperature increases. For example, leaf temperature is equal to air temperature at an air temperature of 25 °C and 30% relative humidity. Relative humidity greater than this value creates conditions in which the leaf is warmer than the air. At a temperature of 35 °C, leaf temperature is greater than air temperature only for relative humidity greater than 70%. In a hot environment, the leaf is cooler than air for all but the most humid conditions. In a cool environment, the leaf is warmer than air for all but the most arid conditions. The cooling effect of evaporation is why we sweat, and it is why a person may feel comfortable in dry climates, where low relative humidity results in rapid evaporation of sweat, but hot and uncomfortable in humid climates, where evaporation is not as efficient.

## 16.5 Leaf-air coupling

The leaf environment is coupled to the surrounding air through a resistance network that regulates sensible

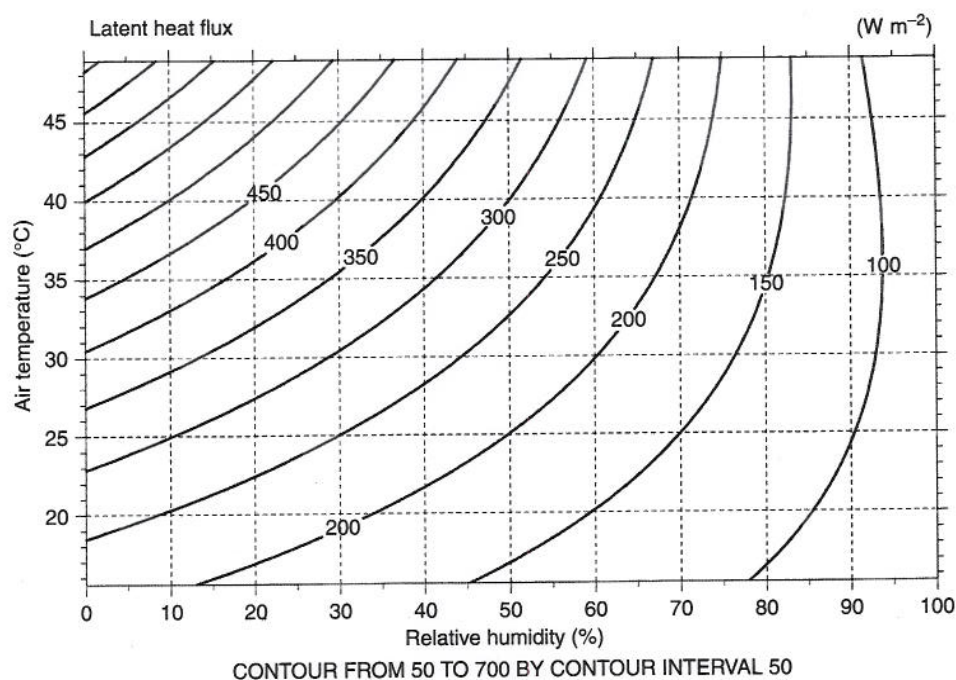
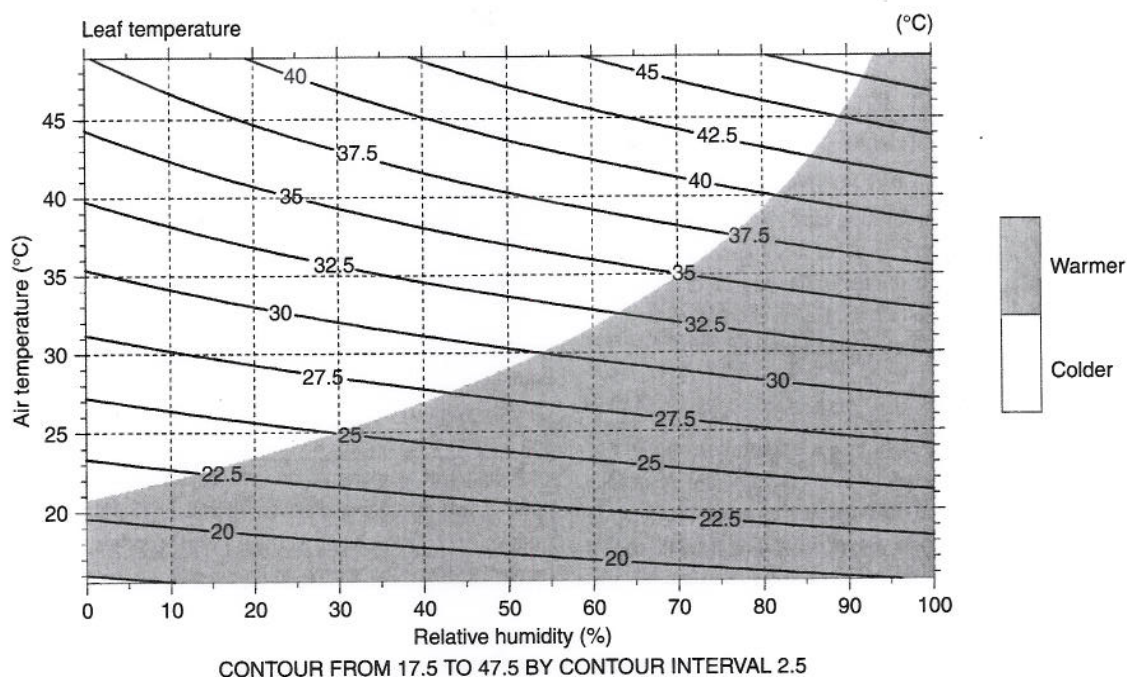


FIGURE 16.4. Leaf temperature (top) and latent heat flux (bottom) in response to air temperature and relative humidity. The gray region shows combinations of air temperature and relative humidity where the leaf is warmer than the air. Leaf temperature and latent heat flux are calculated from (16.2). The radiative forcing is  $Q_g = 700 \text{ W m}^{-2}$ , winds are light ( $u = 0.9 \text{ m s}^{-1}$ ), and other factors are as in Table 16.1.

and latent heat fluxes (Fig. 16.2). Sensible heat flux is inversely proportional to the boundary layer resistance. Latent heat flux is inversely proportional to the boundary layer and stomatal resistances acting in series.

The Penman–Monteith equation (13.18) extended to a leaf (Monteith 1965) gives important insights to the degree to which these resistances regulate the coupling between leaf and air. For a leaf,  $G=0$  and the



resistances  $r_H$  and  $r_W$  are replaced with  $r_b/2$  and  $r_s + r_b$ , respectively:

$$\lambda E = \frac{sR_n + \rho C_p(e_s[T_a] - e_a)/(r_b/2)}{s + \gamma(r_s + r_b)/(r_b/2)} \quad (16.8)$$

The role of stomata in regulating leaf transpiration can be seen in the two limiting cases when leaf boundary layer resistance is very large or very small (Jarvis and McNaughton 1986). If the leaf boundary layer resistance becomes very large, so that the leaf is decoupled from the surrounding air by a thick boundary layer:

$$\lambda E = sR_n/(s + \gamma) \quad (16.9)$$

which is known as the equilibrium evaporation rate. In this case, transpiration is independent of stomatal resistance and depends chiefly on the net radiation available to evaporate water. If the boundary layer resistance is small, so that there is strong coupling between conditions at the leaf surface and outside the leaf boundary layer, transpiration is at a rate imposed by stomatal resistance:

$$\lambda E = \rho C_p(e_s[T_a] - e_a)/(\gamma r_s) \quad (16.10)$$

In this case, an increase or decrease in stomatal resistance causes a proportional decrease or increase in transpiration. In between these two extremes of equilibrium and imposed transpiration, intermediate degrees of stomatal control prevail. The degree of coupling between a leaf and surrounding air depends on leaf size and wind speed (Fig. 16.3). Small leaves, with low boundary layer resistance, approach strong coupling. Large leaves, with high boundary layer resistance, are weakly coupled. Leaves in still air are decoupled from the surrounding air while moving air results in strong coupling.

## 16.6 Leaf size and shape

Principles of water use efficiency and heat and gas exchange result in an optimal leaf form for a given environment. The temperature of a leaf is regulated by heat and moisture exchange with the surrounding air. Under sunny conditions, high sensible heat exchange decreases leaf temperature; low sensible heat exchange creates a warmer temperature. Loss of water during transpiration also decreases leaf temperature because of the large amount of energy needed to change water from liquid to vapor. The ease with which heat and moisture are lost from a leaf is determined in part by leaf size and shape.

Leaf size and shape greatly influence boundary layer resistance. A small leaf has a lower boundary layer resistance to heat and moisture transfer than does a large leaf (Fig. 16.3). This is because a small leaf has relatively little

surface area relative to its perimeter length. Consequently, small leaves have a thin boundary layer and efficient heat transfer. Conditions at the leaf surface are closely coupled to the air, and leaf temperature is similar to that of the surrounding air. In contrast, a large leaf has a large surface area relative to perimeter length. Large leaves have a thick boundary layer, high boundary layer resistance, and inefficient heat transfer. They are decoupled from the surrounding air so that leaf temperature is several degrees warmer than that of air. Similarly, deep lobes on leaves decrease the surface area relative to perimeter length, resulting in smaller boundary layer resistance than leaves without lobes.

Observations and theoretical studies show that the size and shape of leaves are a compromise among leaf energy exchange, leaf temperature, and photosynthesis. There is an optimal leaf size for a given environment (Parkhurst and Loucks 1972; Givnish and Vermeij 1976; Woodward 1993). Leaves growing in sunny environments are smaller and more deeply lobed than leaves growing in shaded environments. Leafy plants growing in hot, arid desert environments or cold arctic and alpine environments have small leaves. In part, this is related to the influence of leaf dimension on leaf boundary layer resistance and the efficiency with which heat and moisture are transported away from a leaf.

Under the assumption that leaf size is determined so as to maximize water use efficiency, Parkhurst and Loucks (1972) showed that large leaves are favored in warm to hot climates with low light conditions, such as might be found in the understory of temperate and tropical forests (Fig. 16.5).

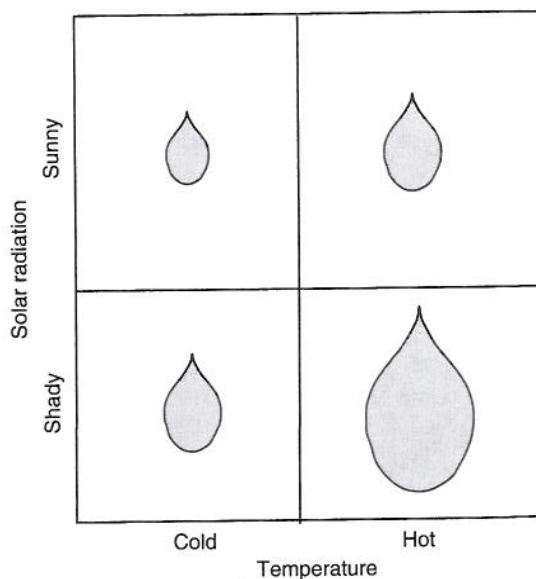


FIGURE 16.5. Leaf size in relation to solar radiation and temperature. Adapted from Parkhurst and Loucks (1972).



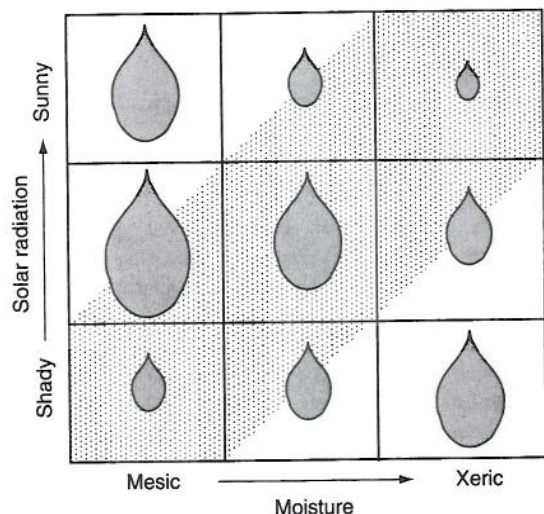


FIGURE 16.6. Leaf size in relation to solar radiation and moisture. The stippled area shows the habitats likely in nature and between the forest understory and overstory. Adapted from Givnish and Vermeij (1976).

Small leaves are favored in sunny environments (e.g., the forest overstory) and in cold climates. Givnish and Vermeij (1976) examined the influence of moisture on leaf size. They found large leaves are expected in the humid, shaded environment of the forest understory while small leaves occur in the sunny, dry conditions of the forest overstory (Fig. 16.6). In a sunny environment, large leaf size increases transpiration so that large leaves are favored only in mesic conditions. Conversely, large leaves impede transpiration in a shaded environment; small leaves are favored with increasingly moist conditions.

The effect of energy exchange and stomata on leaf form is seen in the fossil record. Early vascular plants were leafless or had short cylindrical leaves. Some 40 million years passed between the appearance of the first land plants and the origin of flat leaves that resemble those of modern plants. This may be related to high atmospheric  $\text{CO}_2$  concentrations that prevailed during early plant life (Beerling *et al.* 2001; Beerling and Berner 2005). In a  $\text{CO}_2$ -enriched atmosphere, plants needed fewer stomata to absorb  $\text{CO}_2$  for photosynthesis. However, broad flat leaves with a low density of stomata are prone to overheating. The appearance of broad leaves is associated with a 90% decline in atmospheric  $\text{CO}_2$ . Plants developed more stomata as atmospheric  $\text{CO}_2$  declined, which allowed flat leaves to stay cool. Leaf form may also have led to the extinction of many plant species 200 million years ago (McElwain *et al.* 1999; Beerling and Berner 2005). The fossil record shows species with large entire leaves were replaced by species with smaller, more dissected leaves. An increase in

atmospheric  $\text{CO}_2$  at this time warmed climate. The temperature of large leaves with entire margins (i.e., no lobes) reached lethal levels in this warm climate. Small or highly lobed leaves had lower temperatures and thus had an advantage over large leaves in warm climates.

These studies suggest a strong relationship between leaf morphology and environment. The close relationship among the size of leaves, leaf shape, and leaf edges (e.g., smooth, serrated, lobed) with temperature and precipitation is one means to reconstruct past climate from fossil leaves (Wolfe 1995; Wilf 1997, 2000; Wilf *et al.* 1998; Wolfe *et al.* 1998).

## 16.7 Review questions

In questions 3–6, use the following values for the Penman–Monteith equation unless otherwise noted:  $e_s[T_a] = 3169$  Pa and  $s = 189$  Pa  $^{\circ}\text{C}^{-1}$  (values for  $T_a = 25^{\circ}\text{C}$ ); relative humidity, 75%;  $\rho = 1.15$  kg  $\text{m}^{-3}$ ;  $C_p = 1005$  J  $\text{kg}^{-1}^{\circ}\text{C}^{-1}$ ; and  $\gamma = 66.5$  Pa  $^{\circ}\text{C}^{-1}$ .

1. Derive the conversion factor between resistance in units  $\text{s m}^{-1}$  and units  $\text{m}^2 \text{s mol}^{-1}$ .
2. Calculate leaf resistance to transpiration for: (a) a flat leaf with stomata on one side and (b) a flat leaf with stomata on both sides.  $r_b = 20$   $\text{s m}^{-1}$  and  $r_s = 200$   $\text{s m}^{-1}$ .
3. Use the Penman–Monteith equation for a leaf to calculate  $\lambda E$ ,  $H$ , and  $T_s - T_a$  for the following stomatal resistance and net radiation:  $r_s = 100$   $\text{s m}^{-1}$  and  $r_s = 500$   $\text{s m}^{-1}$ ;  $R_n = 500$   $\text{W m}^{-2}$  and  $R_n = 1000$   $\text{W m}^{-2}$ . Leaf size is  $d = 3$  cm and stomata are on one side of the leaf. Use  $u = 3$   $\text{m s}^{-1}$ . How does transpiration affect leaf temperature? How does this vary with net radiation?
4. Use the Penman–Monteith equation for a leaf to calculate  $T_s - T_a$  for the following conditions with  $R_n = 750$   $\text{W m}^{-2}$  (sunny),  $u = 0.1$   $\text{m s}^{-1}$  (calm wind), and  $r_s = 5000$   $\text{s m}^{-1}$  (low transpiration). Then determine which is more effective at reducing leaf temperature: (a) shade,  $R_n = 250$   $\text{W m}^{-2}$ ; (b) wind,  $u = 1$   $\text{m s}^{-1}$ ; (c) transpiration,  $r_s = 100$   $\text{s m}^{-1}$ ; or (d) shade, wind, and transpiration. Leaf size is  $d = 5$  cm and stomata are on one side of the leaf.
5. Use the Penman–Monteith equation for a leaf to calculate  $T_s - T_a$  for the following values of leaf size and stomatal resistance:  $d = 0.75$  cm and  $d = 12$  cm;  $r_s = 100$   $\text{s m}^{-1}$  and  $r_s = 500$   $\text{s m}^{-1}$ . How does leaf–air coupling vary with leaf size and stomatal resistance? Use  $R_n = 500$   $\text{W m}^{-2}$  and  $u = 3$   $\text{m s}^{-1}$ .
6. Use the Penman–Monteith equation for a leaf to calculate  $\lambda E$ ,  $H$ , and  $T_s - T_a$  for the following leaf size, stomatal resistance, and net radiation:  $d = 3$  cm and  $d = 10$  cm;  $r_s = 100$   $\text{s m}^{-1}$  and  $r_s = 5000$   $\text{s m}^{-1}$ ;

$R_n = 250 \text{ W m}^{-2}$  and  $R_n = 750 \text{ W m}^{-2}$ . In a sunny environment, which leaf is favored (based on temperature)? How does leaf temperature differ between the small and large leaf in a shaded environment? How does stomatal resistance affect these conclusions? Use  $u = 3 \text{ m s}^{-1}$  and  $r_s = 100 \text{ s m}^{-1}$  (one-sided) for a mesic environment and  $r_s = 5000 \text{ s m}^{-1}$  (one-sided) for a dry environment.

## 16.8 References

- Beerling, D. J. and R. A. Berner, 2005. Feedbacks and the co-evolution of plants and atmospheric  $\text{CO}_2$ . *Proceedings of the National Academy of Sciences, USA*, **102**, 1302–5.
- Beerling, D. J., C. P. Osborne, and W. G. Chaloner, 2001. Evolution of leaf-form in land plants linked to atmospheric  $\text{CO}_2$  decline in the Late Palaeozoic era. *Nature*, **410**, 352–4.
- Campbell, G. S. 1977. *An Introduction to Environmental Biophysics*. Springer-Verlag, 159 pp.
- Campbell, G. S. and J. M. Norman, 1998. *An Introduction to Environmental Biophysics*, 2nd edn. Springer-Verlag, 286 pp.
- Gates, D. M., 1980. *Biophysical Ecology*. Springer-Verlag, 611 pp.
- Givnish, T. J. and G. J. Vermeij, 1976. Sizes and shapes of liane leaves. *American Naturalist*, **110**, 743–78.
- Jarvis, P. G. and K. G. McNaughton, 1986. Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research*, **15**, 1–49.
- Jones, H. G., 1992. *Plants and Microclimate: a Quantitative Approach to Environmental Plant Physiology*, 2nd edn. Cambridge University Press, 428 pp.
- McElwain, J. C., D. J. Beerling, and F. I. Woodward, 1999. Fossil plants and global warming at the Triassic–Jurassic boundary. *Science*, **285**, 1386–90.
- Monteith, J. L., 1965. Evaporation and environment. In *The State and Movement of Water in Living Organisms (19th Symposium of the Society for Experimental Biology)*, ed. G. E. Fogg. Academic Press, pp. 205–34.
- Monteith, J. L. and M. H. Unsworth, 1990. *Principles of Environmental Physics*, 2nd edn. Edward Arnold, 291 pp.
- Parkhurst, D. F. and O. L. Loucks, 1972. Optimal leaf size in relation to environment. *Journal of Ecology*, **60**, 505–37.
- Wilf, P., 1997. When are leaves good thermometers? A new case for leaf margin analysis. *Paleobiology*, **23**, 373–90.
2000. Late Paleocene–early Eocene climate changes in southwestern Wyoming: paleobotanical analysis. *Geological Society of America Bulletin*, **112**, 292–307.
- Wilf, P., S. L. Wing, D. R. Greenwood, and C. L. Greenwood, 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. *Geology*, **26**, 203–6.
- Wolfe, J. A., 1995. Paleoclimatic estimates from tertiary leaf assemblages. *Annual Review of Earth and Planetary Sciences*, **23**, 119–42.
- Wolfe, J. A., C. E. Forest, and P. Molnar, 1998. Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America. *Geological Society of America Bulletin*, **110**, 664–78.
- Woodward, F. I., 1993. Leaf responses to the environment and extrapolation to larger scales. In *Vegetation Dynamics and Global Change*, ed. A. M. Solomon and H. H. Shugart. Chapman and Hall, pp. 71–100.