



# Transpiration and the Ascent of Sap

## INTRODUCTION

Fiscus and Kaufmann (in Stewart and Nielsen, 1990) commented that much of what is discussed as plant water relations deals with water movement in the soil-plant-atmosphere continuum (SPAC). It ranges from movement as molecules in diffusion from cell to cell and as vapor in transpiration, to movement of bulk water solution in mass flow of the transpiration stream from roots to shoots through the xylem. Movement of water in cells was discussed in Chapter 3, movement of soil water in Chapter 4, and the absorption of water in Chapter 6. This chapter discusses the loss of water by transpiration and the resulting movement of water and solutes by mass flow through the xylem to transpiring surfaces of shoots.

## The Importance of Transpiration

Transpiration is the loss of water from plants in the form of vapor and it is the dominant process in plant water relations because of the large volume of water involved and its controlling influence on plant water status. It also produces the energy gradient that largely controls absorption and the ascent of sap. In warm sunny weather, transpiration often causes transient midday wilting and as the soil dries it causes permanent wilting and finally death by dehydration if the soil moisture is not replenished by rain or irrigation. Worldwide, more plants probably are injured or killed by dehydration caused by excessive transpiration than by any other single cause.

**Table 7.1** Relative Water Losses by Transpiration and Evaporation from an Illinois Cornfield during the Period from Mid-June to Early September

Year	Total evapo- transpiration from uncovered plot (cm)	Transpiration from covered plot (cm)	Transpiration as percentage of evapotran- spiration	Total precipitation (cm)	Excess of evapotranspiration over rainfall (cm)
1954	32.25	16.5	51%	18.5	13.75
1955	34.50	17.5	51%	23.0	11.50
1957	33.75	15.1	45%	24.0	9.75

<sup>a</sup>From Peters and Russell (1959).

The quantitative importance of transpiration is indicated by the fact that a well-watered Kansas corn plant loses about 200 liters of water during a growing season or nearly 1300 tons per acre (= 475 metric tons per hectare or about 28 cm of water) (Miller, 1938, p. 412). An Illinois corn field transpired an amount of water equal to 60 to 90% of the precipitation during the growing season (Peters and Russell, 1959) and the combined evaporation from the soil and transpiration from the crop (evapotranspiration) exceeded the precipitation during the growing season, as shown in Table 7.1. In contrast, a deciduous forest in the more humid southern Appalachians transpired 40 to 55 cm per year, which used only 25 to 35% of the annual precipitation (Hoover, 1944), as shown in Table 7.2.

Several hundred grams of water are required to produce a gram of plant dry matter (Table 7.3), but about 95% of this is lost in transpiration. If it were not for the water dissipated by transpiration, a crop could be grown with the water

**Table 7.2** Amounts of Water Lost in Various Ways by a North Carolina Watershed Covered with a Deciduous Forest (1940-1941) and the Increase in Runoff Which Followed Cutting of All Woody Vegetation and Elimination of Transpiration (1941-1942)<sup>a</sup>

Process	1940-1941	1941-1942
Precipitation	158.0	158.4
Interception	16.6	9.5
Runoff	53.4	93.0
Soil storage	-0.4	9.7
Evaporation	39.7	46.0
Transpiration	48.7	00.0

Note. Data in centimeters.

<sup>a</sup>From Hoover (1944).

**Table 7.3** Water Requirement or Transpiration Ratio in Grams of Water per Gram Dry Matter for the Years 1911–1917 at Akron, Colorado, and the Evaporation from a Free Water Surface from April to September 1<sup>a</sup>

Plant	1911	1912	1913	1914	1915	1916	1917
Alfalfa	1068	657	834	890	695	1047	822
Oats, Burt	639	449	617	615	445	809	636
Barley, Hannchen	527	443	513	501	404	664	522
Wheat, Kubanka	468	394	496	518	405	639	471
Corn, N. W. Dent	368	280	399	368	253	495	346
Millet, Kursk	287	187	286	295	202	367	284
Sorghum, Red Amber	298	239	298	284	303	296	272
Evaporation: April 1 to September 1 (mm)	1239	957	1092	1061	848	1196	1084

<sup>a</sup>From Miller (1938).

supplied by a single rain or irrigation, assuming that evaporation from the soil was controlled by mulching.

It sometimes is argued that transpiration is beneficial because it cools leaves, accelerates the ascent of sap, and increases the absorption of minerals (Clements, 1934; Gates, 1968). Rapidly transpiring leaves usually are cooler than slowly transpiring leaves (Gardner *et al.*, 1981), but leaves in the sun rarely are seriously overheated even when transpiration is reduced by wilting. Water moves to the tops of plants as they grow and transpiration merely increases the quantity and speed of movement. Absorption of minerals probably is increased, but some understory plants thrive in shady, humid habitats where the rate of transpiration is relatively low. Although Winneberger (1958) reported that high humidity reduced plant growth, Hoffman *et al.* (1971), O'Leary and Knecht (1971), and others found that growth generally was better in high than in intermediate or low humidity and Tanner and Beevers (1990) concluded that transpiration is not essential. The numerous harmful effects of water stress caused by rapid transpiration are discussed in later chapters.

Transpiration can be regarded as an unavoidable evil, unavoidable because a leaf structure favorable for uptake of the carbon dioxide necessary for photosynthesis also is favorable for loss of water, and evil because it often causes injury by dehydration. The evolution of a leaf structure favorable for high rates of photosynthesis apparently has had greater survival value in most habitats than one conserving water, but reducing photosynthesis. Thus, the leaf anatomy of most mesophytic plants causes them to live in danger of injury from excessive transpiration. In general, plants adapted to dry environments cannot compete effectively with plants adapted to moist environments when both are well watered (Bunce, 1981; Orians and Solbrig, 1977). The relationship between tran-

spiration and photosynthesis was discussed in detail by Cowan (1982) and is discussed further in Chapters 10 and 12, where research is cited indicating that some varieties of plants that yield well during water deficits also yield well when supplied with water.

## THE PROCESS OF TRANSPIRATION

Transpiration involves two steps, the evaporation of water from cell surfaces into intercellular spaces and its diffusion out of plant tissue, chiefly through stomata and the cuticle and to a lesser extent through the lenticels in stem bark of woody plants.

### Evaporating Surfaces

It usually is assumed that most of the water evaporates from the surfaces of leaf mesophyll cells into the intercellular spaces (Slatyer, 1967, pp. 215–221; Sheriff, 1984). However, it was argued by some writers (Meidner, 1975; Byott and Sheriff, 1976) that much water evaporates from the inner surfaces of epidermal cells in the vicinity of guard cells, or even from the inner surfaces of guard cells, the peristomatal transpiration of Maercker (1965). However, the exposed surface of mesophyll cells usually is 10 to 15 times greater than the exposed inner epidermal surface. Also, Nonami and Schulze (1989) found the water potential of mesophyll cells in transpiring leaves to be lower than that of epidermal cells. The literature on this interesting question has been summarized by Davies (1986, pp. 65–69). Tyree and Yianoulis (1980) made computer studies indicating that 75% or more of the evaporation should occur from near the guard cells, but their calculations assumed that water evaporates equally freely from all mesophyll cell walls. This assumption probably is incorrect because investigators from von Mohl in 1845 to the present have reported the presence of varying amounts of cutin or suberin on the cell walls bordering intercellular space (Lewis, 1945; Scott, 1964; Sheriff, 1977a, 1984). According to Norris and Bukovac (1968), the cuticle covering the outer surface of the lower epidermis of hypostomatous pear leaves (leaves with stomata only on the lower surface) extends in through the stomatal pores and covers the inner surfaces of the guard cells and the adjacent lower epidermis. It seems that the relative importance of evaporation from various internal surfaces in leaves cannot be decided until more information is available concerning the amount of internal cutinization at various distances from stomata. These problems are discussed further in Chapter 11.

After water vapor has diffused into the intercellular spaces it escapes from the leaves by diffusion through the stomata and to a lesser extent through the cuticle, and through lenticels in the bark of twigs of woody plants (Geurten, 1950; Huber, 1956; Schönherr and Ziegler, 1980).

### Driving Forces and Resistances

The rate of transpiration depends on the supply of water at the evaporating surfaces, the supply of energy to vaporize water, the size of the driving forces, and the resistances or conductances in the pathway. The driving force for liquid water is the gradient in water potential, that for water vapor is the difference in vapor concentration or vapor pressure.

Evaporation  $E$  can be described by:

$$E = \frac{C_{\text{water}} - C_{\text{air}}}{r_{\text{air}}}, \quad (7.1)$$

where  $E$  is given in  $\text{g} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ,  $C_{\text{water}}$  and  $C_{\text{air}}$  are given in  $\text{g} \cdot \text{m}^{-3}$  and are vapor concentrations at the evaporating surface and in the bulk air, and  $r_{\text{air}}$  is in  $\text{sec} \cdot \text{m}^{-1}$  and is the resistance of the air boundary layer to water vapor diffusion. Equation (7.1) indicates that the rate of evaporation is proportional to the concentration difference. Doubling the difference will double the rate, all other factors being equal. Evaporation also is influenced by changes in  $r_{\text{air}}$  which can vary as the boundary layer next to the leaf or water surface varies. This layer contains unstirred air through which the vapor moves mostly by diffusion which is slow compared to the rate in wind-stirred air. The thickness of the layer is determined mostly by wind speed and the size of the surface: the faster the wind speed, the thinner the boundary layer and the smaller is  $r_{\text{air}}$  resulting in faster evaporation. Also, the smaller the surface the faster the evaporation.

Equation (7.1) applies at sea level and must be corrected for pressure if it is used elsewhere, as on tall mountains. As a consequence, Eq. (7.1) often is shown with the driving force given as partial pressures ( $e_{\text{water}} - e_{\text{air}}$ ) in units of kPa/kPa instead of concentrations ( $C_{\text{water}} - C_{\text{air}}$ ). This has the advantage that the effects of atmospheric pressure are taken into account explicitly by dividing the vapor pressure of water by the total pressure of the atmosphere. The pressures can be calculated from the concentrations and the rate of evaporation usually is given in  $\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  and the resistance of the boundary layer in  $\text{sec} \cdot \text{m}^2 \cdot \text{mol}^{-1}$ . Otherwise, the equations are fundamentally the same.

In a plant, this process is more complex because water vapor must travel through the leaf. The leaf contains intercellular spaces and stomata, and water vapor moves through them mostly by diffusion before it can enter the boundary layer. This additional resistance makes the rate slower than for a free water surface. The leaf resistance is in series with the boundary layer resistance, and the whole effect can be described by including an additional resistance in the vapor path in which case the rate of transpiration  $T$  is

$$T = \frac{C_{\text{leaf}} - C_{\text{air}}}{r_{\text{leaf}} + r_{\text{air}}}, \quad (7.2)$$

where  $C_{\text{leaf}}$  is the vapor concentration at the evaporating surface inside the leaf and  $r_{\text{leaf}}$  is the diffusive resistance of all the paths for vapor diffusion in the leaf

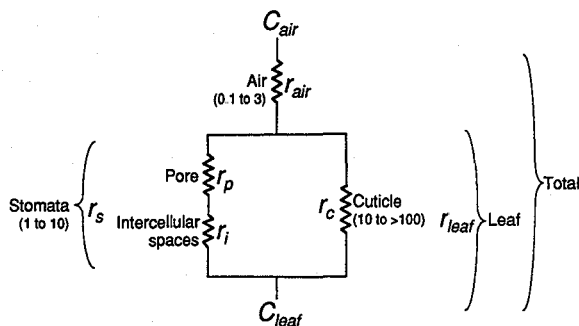


Figure 7.1 Diagram showing approximate resistances in seconds per centimeter to diffusion of water vapor from a leaf. Stomatal and cuticular resistances vary among species and with leaf hydration and atmospheric humidity. The transpiration is proportional to  $(C_{\text{leaf}} - C_{\text{air}})$ , the vapor concentration difference between the leaf and air, and inversely proportional to the resistances in the pathway. From Kramer (1983).

in units of  $\text{sec} \cdot \text{m}^{-1}$  or, for the driving force in pressure units,  $\text{sec} \cdot \text{m}^2 \cdot \text{mol}^{-1}$ . Because  $r_{\text{leaf}}$  causes  $T$  to be less than  $E$  when the other factors are maintained constant, one can evaluate  $r_{\text{leaf}}$  by comparing the rate of transpiration of a leaf with the rate of evaporation of a comparably shaped piece of wet filter paper. The leaf will always lose water more slowly than the paper and the magnitude of  $r_{\text{leaf}}$  can be calculated from the difference. Note that a leaf with closed stomata will have a larger  $r_{\text{leaf}}$  than it will with open stomata and the rate of transpiration will be slower.

The resistance of a leaf can be divided into a number of component resistances as shown in Fig. 7.1, and some species differences in cuticular and stomatal resistance are shown in Table 7.4. If most or all of the stomata are on one surface,  $r_{\text{leaf}}$  will be quite different for the upper (adaxial) and lower (abaxial)

Table 7.4 Resistance to Movement of Water Vapor through the Boundary layer ( $r_a$ ), Stomata ( $r_s$ ), and Cuticle ( $r_c$ ) in Leaves of Several Species<sup>a</sup>

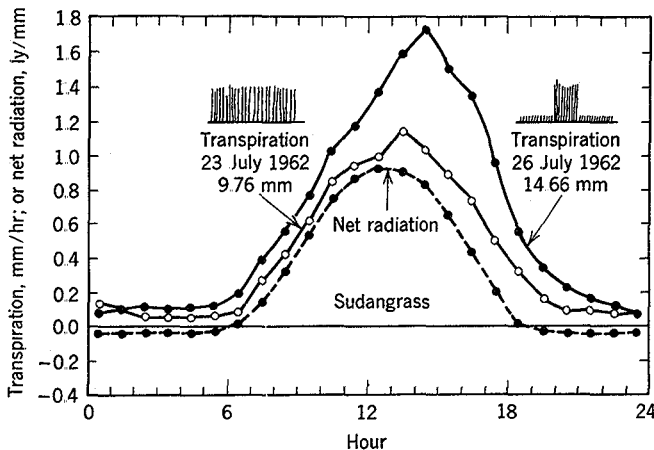
Species	Resistance to water vapor ( $\text{sec} \cdot \text{cm}^{-1}$ )		
	$r_a$	$r_s$	$r_c$
<i>Betula verrucosa</i>	0.80	0.92	83
<i>Quercus robur</i>	0.69	6.7	380
<i>Acer platanoides</i>	0.69	4.7	85
<i>Circaea lutetiana</i>	0.61	16.1	90
<i>Lamium galeobdolon</i>	0.73	10.6	37
<i>Helianthus annuus</i>	0.55	0.38	—

<sup>a</sup>From Holmgren *et al.* (1965).

surfaces. Also the stomata on the upper and lower surfaces often differ in their reaction to light and water stress (Pallardy and Kozlowski, 1979; Sanchez-Diaz and Kramer, 1971, for example), as shown in Fig. 8.8. There are measurable differences in temperature in different parts of transpiring leaves, reflecting local differences in rate of air movement from the margin inward (Cook *et al.*, 1964; Hashimoto *et al.*, 1984).

### Energy Relations

The energy required to evaporate water from leaves and plants comes from direct solar radiation, from radiation reflected or reradiated from the soil and surrounding objects, and from the flow of sensible heat between the leaf and the environment. Sensible heat is transferred because of temperature differences between plants and the surrounding air, and it moves by diffusion, convection, and advection. Diffusive heat transfer occurs in unstirred air and is observed when there are temperature differences across the boundary layer of unstirred air next to leaves and other surfaces. Convection and advection refer to heat transfer by the movement of air in bulk due to temperature-induced density differences or horizontal wind movement. Convection can be seen in the warm air rising from a warm surface such as a radiator and advection in the winds that bring new air into a plant canopy. An example of the increase in transpiration caused by increased advection resulting from the removal of surrounding vegetation is shown in Fig. 7.2. Sensible heat transfer is positive or negative,



**Figure 7.2** The "oasis effect" as shown by the increase in transpiration from a lysimeter in a closed stand of Sudan grass after removal of the surrounding crop, exposing the plants in the lysimeter. Although radiation was similar on the 2 days, additional energy supplied by increased exposure to air movement and advection resulted in a much higher transpiration after the plot was exposed. From Kramer (1983), after Van Bavel *et al.* (1963).

positive when the leaves are cooler than the air, negative when they are warmer, as in the evening or when suddenly shaded. When transpiration occurs, liquid water changes state and energy is required even though no change in the temperature of the evaporated water is involved. In effect, the latent heat for evaporation is extracted from energy in the molecules that stay behind in the liquid.

When there is condensation, the reverse occurs and the latent heat is released to the surrounding molecules. The ratio of heat transferred as sensible heat to that transferred as latent heat by transpiration is called the Bowen ratio (see Nobel, 1991, p. 483).

The energy budget for a leaf can be partitioned as

$$R_n + H + E_e = 0, \quad (7.3)$$

where the  $R_n$  (net radiation) is the net flux of radiation actually absorbed by the leaves and consists of the total solar radiation plus that from the environment, minus reflected radiation and that reradiated.  $H$  is the sensible heat flux between the leaves and the environment, and  $E_e$  is the latent heat lost by evaporation of water or gained by condensation. Each term refers to the rate of energy transferred per unit of projected leaf area (the flux) and the fluxes in the equation are large by comparison with the energy for photosynthesis and respiration so these effects are ignored. In this equation, each term can be positive or negative depending on whether energy moves toward or away from the leaf, and the various terms add to zero, that is, the energy budget is in balance whenever leaf temperature is constant. When the energy budget changes, leaf temperature quickly adjusts and stabilizes at the new condition dictated by the equation.

The energy budget is important for understanding the behavior of transpiration. If any two terms in the equation are known, the other can be calculated. For example, during the daytime when the leaves are irradiated by the sun,  $R_n$  is positive and  $E_e$  is negative because transpiration is occurring. Occasionally the positive  $R_n$  just balances the negative  $E_e$ . In this situation, the  $H$  becomes zero because no sensible heat transfer occurs, and the leaf has the same temperature as the air. Usually, however,  $R_n$  is not balanced by  $E_e$  and leaf temperatures differ from air temperatures. Even in controlled environments leaves rarely have the same temperature as the air. Thus, it is usual for sensible heat transfer to occur to or from leaves, depending on whether their temperature is lower or higher than that of the air.

Similar principles operate at night.  $R_n$  is negative because leaves radiate to the cold night sky and are not receiving input from the sun.  $E_e$  also is negative because of transpiration, particularly early in the evening. Both of these negative fluxes tend to decrease leaf temperature.  $H$  becomes positive and balances the equation. The air conducts sensible heat to the cool leaf whose temperature stabilizes at a cooler temperature. If the leaf is cold enough, dew condenses on the leaf or frost forms. The condensation releases latent heat that helps to pre-



vent further temperature depression of the leaf. This explains why dew is most likely to be heavy on a cloudless night when the night sky is clear and leaves lose the most energy by radiation. Clouds obscure the distant sky because of the water vapor and the water droplets they contain.

Many other aspects of transpirational behavior can be explained by an analysis of leaf energy budgets and the causes of the variations in each term constitute a field of study in their own right. Readers are referred to Gates (1968, 1980), Knoerr (1967), and Nobel (1991, Chapter 7) for more detailed discussions.

### Vapor Pressure Gradients

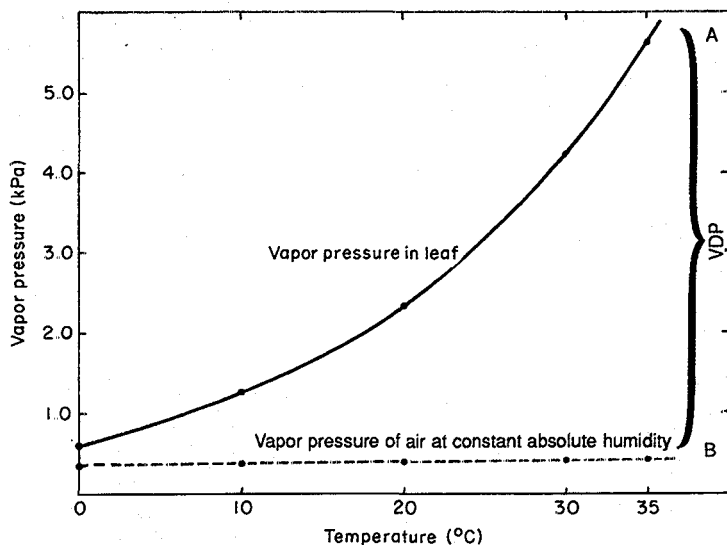
The driving force causing water vapor to move out of plants or from other evaporating surfaces is the difference between the vapor pressure of the evaporating surface and the humidity or vapor pressure of water in the bulk air. The humidity and vapor pressure of bulk air depend on its water content and its temperature, while those of the evaporating surface of plants depend on the water potential and temperature. The water potential of fully turgid plant tissue is zero, but the tissues of rapidly transpiring plants often have water potentials of  $-1.0$  MPa or less. However, as shown in Table 7.5, a large reduction in cell water potential causes only a small reduction in vapor pressure. For example, at  $30^{\circ}\text{C}$  and a cell water potential of  $-3.0$  MPa the vapor pressure of the cell sap is 98% of the vapor pressure of pure water. Thus, a large reduction in cell water potential has little effect on the rate of evaporation from the cell surface.

*Relative and Absolute Humidity.* Weather reports emphasize the relative humidity of the atmosphere, which is the water content as a percentage of that at saturation at the same temperature, instead of the absolute humidity, which

**Table 7.5** The Vapor Pressure of Water ( $e$ ), the Vapor Pressure at Cell Surfaces at Three Cell Water Potentials, and the Difference in Vapor Pressure ( $\Delta e$ ) between Cells and Air at Relative Humidities of 80 and 50% at  $30^{\circ}\text{C}$ <sup>a</sup>

$\Psi_w$ of water and of mesophyll cells (MPa)	$e$ at cell surfaces (kPa)	$\Delta e$ at 80% relative humidity (kPa)	$\Delta e$ at 50% relative humidity (kPa)
0.0	4.243	0.849	2.121
-1.5	4.200	0.806	2.079
-3.0	4.158	0.764	2.037
-6.0	4.073	0.679	1.952

<sup>a</sup> The relative effect of a low  $\Psi_w$  diminishes as the relative humidity decreases. All vapor pressures are for  $30^{\circ}\text{C}$ .



**Figure 7.3** Effect of increasing air and leaf temperatures on vapor pressure deficit (VPD) from leaf (A) to air (B), assuming that the air in the leaf is saturated, but the absolute humidity of the atmosphere at 0°C remains unchanged. The saturation vapor pressure at the evaporating surfaces in the leaf increases over 900% over this temperature range, but the vapor pressure of the water in the atmosphere increases only about 13%, in proportion to the increase in absolute temperature. Thus, there is a rapid increase in vapor pressure deficit, evaporation, and transpiration, as shown by the increasing spread between lines A and B.

is the actual water content in  $\text{g} \cdot \text{m}^{-3}$ . Other things being equal, the rates of evaporation and transpiration are proportional to the size of the absolute humidity difference or vapor pressure difference (Bange, 1953; Cole and Decker, 1973), as shown in Fig. 7.3. A relative humidity of 50% at 20°C must be increased to 75% at 30°C to maintain the same vapor pressure difference and the same rate of evaporation. If the relative humidity were kept at 50% at both 20° and 30°C, the rate of evaporation would be about 80% greater at 30°C than at 20°C because the vapor pressure of liquid water increases much more than the vapor pressure of the water in the air (Fig. 7.3). Table 7.6 shows that increasing the temperature from 20° to 30°C increases the vapor pressure difference about 140%, although it decreases the relative humidity over 40%.

A related problem is that air temperature and leaf temperature often are different and the use of relative humidity, which is defined for identical temperatures, does not accurately describe the vapor pressure difference. Because the vapor pressure difference takes the temperature differences into account (Fig. 7.3), it avoids this problem. The adjustment of atmospheric moisture in growth chambers and other closed containers to maintain similar rates of

**Table 7.6** Effect of Increasing Temperature of Leaf and Air on Vapor Pressure Gradient from Leaf to Air, with Relative Humidity of 80% at 10°C and No Change in Absolute Humidity from that at 10°C

	Leaf and air temperature (°C)		
	10	20	30
Relative humidity of air in %	80	43	30
Vapor pressure at evaporating surface of leaf (kPa)	1.228	2.339	4.246
Vapor pressure in air (kPa)	0.981	1.015	1.051
Vapor pressure gradient from leaf to air (kPa)	0.247	1.324	3.196

evaporation or transpiration at various temperatures requires that the vapor pressure difference between the evaporating surface and the air be the same at all temperatures. Basing the humidity setting of a growth chamber on absolute humidity at air temperature will give a first approximation, but basing the setting on air and leaf temperatures will give a better one.

Estimation of the vapor pressure difference between the interior of leaves and the surrounding air usually assumes that the vapor pressure of water in the cell wall surfaces is that of pure water. This is not exactly correct, as leaf water potential usually is less than zero. However, as indicated earlier in Table 7.5, even fairly low water potentials have little effect on the vapor pressure ( $e$ ) at cell surfaces. The air in the intercellular spaces presumably is approximately saturated when the stomata are closed, but when they are open it usually is below saturation because water vapor is diffusing out (Nobel, 1991, pp. 419–421; Ward and Bunce, 1986).

### Resistances to Diffusion

Two groups of resistances affect transpiration: the internal resistances in plants and the external or boundary layer resistances in their immediate environment.

**Leaf Resistances.** The diffusive resistances of a leaf are shown in Fig. 7.1. The total internal resistance ( $r_{\text{leaf}}$ ) is composed of cuticular resistance ( $r_c$ ) and stomatal resistance ( $r_s$ ) which consists of resistance in intercellular space ( $r_i$ ) and resistance in stomatal pores ( $r_p$ ).

Because stomatal and cuticular resistances are in parallel, an equation for total leaf resistance involves their reciprocals:

$$\frac{1}{r_{\text{leaf}}} = \frac{1}{r_c} + \frac{1}{r_s}. \quad (7.4)$$

The components of stomatal resistance are in series and can be described by their sum:

$$r_s = r_i + r_p. \quad (7.5)$$

The cuticular resistance varies widely among species, as indicated in Table 7.4, but when stomata are open,  $r_s$  is so much lower than  $r_c$  that most water vapor escapes through the stomata, and transpiration is largely controlled by stomatal aperture. Stomatal behavior is discussed in Chapter 8.

There has been considerable discussion of the importance of the mesophyll resistance with respect to transpiration (Kramer, 1969, pp. 306–309; Slatyer, 1967, pp. 256–260). Early in this century Livingston and Brown (1912) observed a decrease in transpiration of rapidly transpiring plants when no decrease in stomatal aperture occurred and attributed it to an increase in mesophyll resistance caused by retreat of the water menisci into the pores of the mesophyll cell walls, reducing the vapor pressure at the evaporating surfaces. This decreases the driving force in addition to increasing the resistance. Evidence for an increase in mesophyll resistance was reported by Shimshi (1963b) and Jarvis and Slatyer (1970), but neither Weatherspoon (1968) nor Jones and Higgs (1980) found significant increases.

Few data are available concerning the relationship between the intercellular space volume of leaves and the rate of transpiration, but a large volume should decrease  $r_i$  (Jarvis *et al.*, 1967). Measurement of the resistance in intercellular spaces with pressure flow porometers indicates that  $r_i$  can be a significant component of the total leaf resistance when the stomata are open (Jarvis and Slatyer, 1970). It increases as leaves are dehydrated because leaf shrinkage causes a decrease in the size of intercellular spaces, which may account for some of the reports of mesophyll resistance. The  $r_i$  can be expected to be larger in thick than in thin leaves. According to Stålfelt (1956b) the intercellular air space varies from 70% of the leaf volume in shade leaves to 20% in sun leaves.

The total resistance for  $\text{CO}_2$  is greater than for water vapor (Gaastra, 1959; Holmgren *et al.*, 1965) because of its larger molecules and the longer diffusion path to the reaction site in chloroplasts (Nobel, 1991, pp. 425–428) which includes diffusion through the liquid phase of the cell. This additional mesophyll resistance for  $\text{CO}_2$  is the basis for the assumption that partial closure of stomata will reduce transpiration more than it reduces photosynthesis. This is discussed in Chapter 12 in connection with water use efficiency and the use of antitranspirants.

*External or Boundary Layer Resistances.* Wind. The boundary layer resistance depends chiefly on wind speed and leaf size and shape for individual

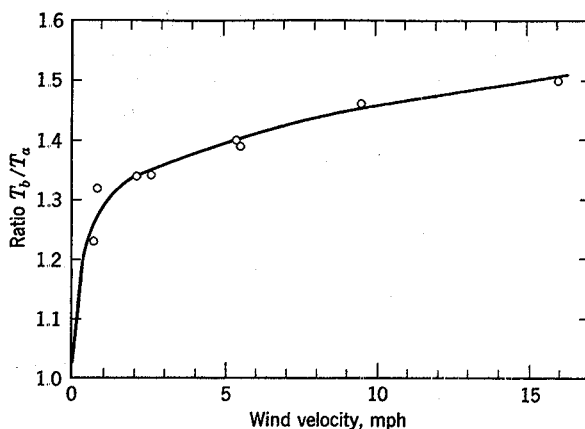


Figure 7.4 Effect of increasing velocity of air movement on the transpiration rate of potted sunflowers growing in a sunny greenhouse. The ordinate is the ratio of transpiration rate of plants exposed to wind ( $T_b$ ) to the rate of plants in quiet air ( $T_a$ ). Most of the effect occurred at a velocity of less than 2 mph. A velocity of 1 mph equals  $44.69 \text{ cm} \cdot \text{sec}^{-1}$ . From Kramer (1983), after Martin and Clements (1935).

plants and on density of the stand and “roughness” of the canopy surface in stands of plants. The effects of wind on transpiration are complex because while an increase in velocity decreases the boundary layer resistance, it also cools leaves, decreasing the vapor pressure gradient from leaf to air. Most of the increase in transpiration occurs at low velocities as shown in Fig. 7.4. Knoerr (1967) pointed out that although a breeze should increase transpiration of leaves exposed to low or moderate radiation where leaves tend to be near air temperature, with high radiation water-deficient leaves may be warmer than the air and a breeze might reduce transpiration by cooling them. The behavior of leaves of various species in wind is quite variable, as shown in Fig. 7.5. Davies *et al.* (1974) also reported differences among tree seedlings of various species exposed to varying wind velocity. Wind increased transpiration of white ash in all velocities, decreased transpiration of sugar maple, and had no effect on red pine. The differences probably are related chiefly to differences in stomatal behavior (see Chapter 8). Van Gardingen *et al.* (1991) also reported surface abrasion of conifer needles exposed to wind, probably affecting cuticular resistance. The effects of change in wind velocity on plant water balance have been discussed by Kitano and Eguchi (1992b). Other effects of wind on plants are discussed in Chapter 12 of Kozlowski *et al.* (1991), in books by Grace (1977), and by Vogel (1989).

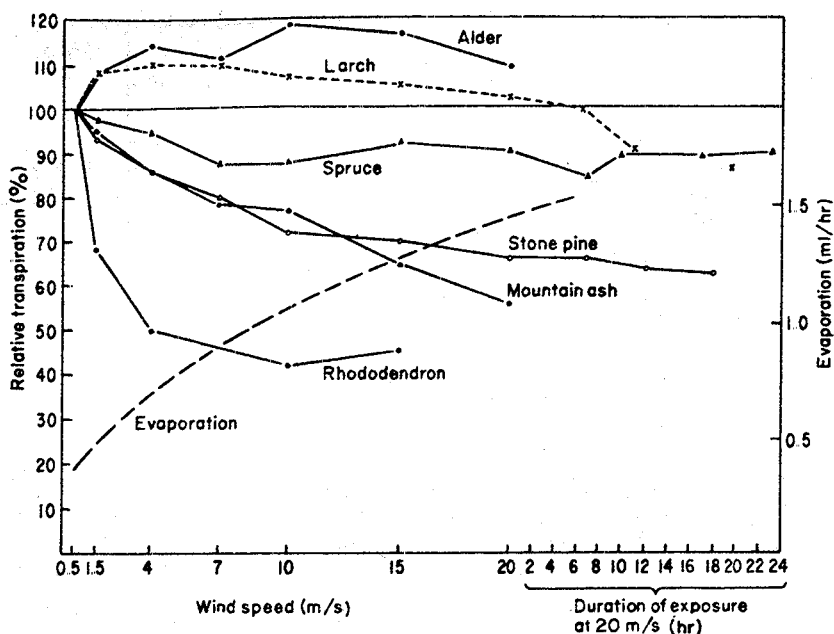


Figure 7.5 Effect of wind velocity on young, potted subalpine plants in a wind tunnel at an air temperature of 20°C, a soil temperature of 15°C, and a light intensity of about 2800 foot candles. Evaporation was measured with a green Piche atmometer. Although evaporation increased steadily with increasing wind velocity, transpiration of most species decreased. From Kramer (1983), after Tranquillini (1969).

## OTHER FACTORS AFFECTING TRANSPIRATION

A few of the specific plant and environmental factors affecting transpiration are discussed briefly. Some of these, such as stomata, are discussed in more detail in other chapters.

### Leaves

**Leaf Temperature and Energy Budget.** The ratio of energy transferred as sensible heat to that dissipated as latent heat by transpiration obviously varies widely and is known as the Bowen ratio. It is said to be about 0.2 for tropical forests, 0.4 to 0.8 for temperate forests, 2 to 6 for semiarid regions, and 10 for deserts (Oke, 1987). According to Idso and Baker (1967), it averages about 0.1 for crops, but can be as high as 6.0 for exposed leaves.

The size, shape, surface characteristics, and exposure of leaves affect the absorption and emission of energy which in turn affect leaf temperature, vapor pressure, and the rate of transpiration. Leaf exposure that is favorable for tran-

spiration also should be favorable for photosynthesis. However, selection for what was believed to be optimum leaf orientation for photosynthesis did not result in any important increase in yield of maize (Loomis *et al.*, 1971). Individual leaf exposure probably decreases in importance in stands of plants.

Leaf temperature affects rates of metabolic processes such as photosynthesis and respiration, but its effects on transpiration are particularly important because it affects the vapor pressure gradient from leaves to the ambient atmosphere, as shown in Fig. 7.3.

In the early part of this century numerous measurements were made of leaf and air temperatures with conflicting results (see Miller, 1938, pp. 472–481), at least partly because of faulty technology. Miller and Saunders (1923), working in Kansas, found that the average leaf temperatures of corn, sorghum, watermelon, and pumpkin were near the temperature of the surrounding air, but that alfalfa leaves were about a degree cooler, probably because of their relatively higher rate of transpiration. Eaton (1930) found transpiring cotton leaves to be about a degree cooler than the air, and young leaves were cooler than older leaves. In contrast, Curtis (1936), working in the cooler, more humid climate of Ithaca, New York, never found leaves cooler than the surrounding air.

In recent decades interest has shifted to canopy temperature as an indicator of plant water stress and as a means of determining differences in development of water stress among cultivars. This was made possible by improvements in infrared thermometry and development of remote sensing methods ranging from observations made from the top of a stepladder to those made by weather satellites. In an early example, Blum *et al.* (1978) used infrared photography to detect differences in drought tolerance of sorghum cultivars because stressed plants were lighter in color than unstressed plants. Jackson (1982) reviewed considerable research on crop canopy temperatures as indicators of water stress and the need for irrigation, and Inoue *et al.* (1990) used leaf temperature measured with an infrared thermometer to estimate the stomatal resistance of cotton. Pinter *et al.* (1990) used midday canopy temperatures to screen wheat cultivars for water use and yield when well watered and when grown with deficit irrigation. It seems likely that leaf temperature will be used more extensively in the future as an indicator of crop water status.

**Leaf Area.** Leaf area is an important factor in both transpiration and photosynthesis. The leaf area of individual plants of course varies from a few square centimeters to many square meters. Leaf areas of stands of plants often are expressed as the leaf area index (LAI) which is the ratio of projected leaf area (area of one surface) to land area bearing the plants. This varies widely from less than 2 for open Eucalyptus forests on dry sites in southeastern Australia (Anderson, 1981) to 16 to 45 for hybrid poplars grown under intensive culture (Isebrands *et al.*, 1977); crop plants are usually about 5 or 6.

**Table 7.7** Transpiration Rates per Unit of Leaf Surface and per Seedling of Loblolly Pine and Hardwood Seedlings for the Period August 22–September 2.<sup>a</sup>

	Loblolly pine	Yellow poplar	Northern red oak
Transpiration ( $\text{g} \cdot \text{day}^{-1} \cdot \text{dm}^{-2}$ )	5.08	9.76	12.45
Transpiration ( $\text{g} \cdot \text{day}^{-1} \cdot \text{tree}^{-1}$ )	106.70	59.10	77.00
Average leaf area per tree ( $\text{dm}^2$ )	21.00	6.06	6.18
Average height of trees (cm)	34.00	34.00	20.00

<sup>a</sup>Average of six seedlings of each species.

Plants and stands of plants with large leaf areas usually transpire more than those with smaller leaf areas, but the decrease in transpiration accompanying reduced leaf area may be partially offset by increased exposure of the remaining leaves, resulting in increased transpiration per unit of leaf area, even though total transpiration is reduced (Parker, 1949). For example, removal of 56% of the trees in a young pine stand reduced transpiration about 33% (Whitehead and Kelliher, 1991a) and removal of 24% of the leaf mass of a *Chamaecyparis* stand reduced transpiration 21% (Morikawa *et al.*, 1986). However, increased exposure of the soil after thinning may increase evaporation from the soil. The large differences in the rate of transpiration per unit of leaf area are sometimes partially compensated by differences in leaf area per plant, as shown in Table 7.7, or by leaf arrangement. For example, there is considerable self shading of needles in clusters of pine needles which reduces photosynthesis and probably transpiration per unit of area (Kramer and Clark, 1947). Sampson and Smith (1993) discussed the influence of such features of canopy architecture as leaf area index, leaf clumping, and canopy gaps on light penetration, and Vogel (1989) discussed leaf shape and size in relation to behavior in wind.

Some woody perennials, such as creosote bush and buckeye, shed most of their leaves when water stressed, greatly reducing the transpiring surfaces (Kozlowski, 1973). The curling or rolling of leaves seen in water-stressed maize, sorghum, and other grasses is said to reduce transpiration by 35 to 75% (Stålfelt, 1956a,b). Leaf orientation and rolling also were discussed by Begg (in Turner and Kramer, 1980) and Clarke (1986). Developmental and seasonal changes in the transpiring surface of leaves were discussed by Killian and Lemée (1956) and Kozlowski (1973) discussed leaf shedding. According to Swank and Douglas (1974), conversion of a North Carolina watershed from deciduous hardwoods to evergreen white pine reduced stream flow.

*Ratio of Roots to Leaves.* The relationship between root surface and leaf surface is particularly important in recently transplanted trees and shrubs where



it often seems desirable to reduce the leaf surface by pruning or defoliation to compensate for the loss of root surface caused by transplanting. However, research by Evans and Klett (1985) indicates that dormant branch pruning of Newport plum (*Prunus cerasifera*) and Sargent crabapple (*Malus sargentii*) at planting time does not affect subsequent overall growth or survival. More research is needed on the effects of root and shoot pruning on trees and shrubs subjected to various degrees of water stress after transplanting. Sometimes the leaves are dipped in or sprayed with an antitranspirant to reduce water loss after transplanting. Use of antitranspirants is discussed in Chapter 12.

**Leaf Size and Shape.** A decrease in leaf size decreases the boundary layer resistance ( $r_a$ ) as shown in Fig. 7.6. Small leaves, the leaflets of compound leaves, and deeply dissected leaves tend to be cooler than large entire leaves because their thinner boundary layers permit more rapid sensible heat transfer. However, the lower boundary layer resistance also is favorable for more rapid water vapor loss so the two effects tend to balance each other (Raschke, 1976).

Parkhurst and Loucks (1972) made an analysis of leaf size in relation to environment based on the assumption that natural selection should have resulted in leaves with maximum water use efficiency in their environment. However, they found many exceptions to their model. Apparently, water use efficiency has not been a major selective force for plants in humid or subhumid environments (Cowan, 1977). Anyway, survival usually depends on possession of a combination of favorable adaptations rather than a single one (Bradshaw, 1965). Furthermore, the importance of leaf size, shape, and orientation tends to decrease in closed stands of plants where the canopy dominates over single leaves.

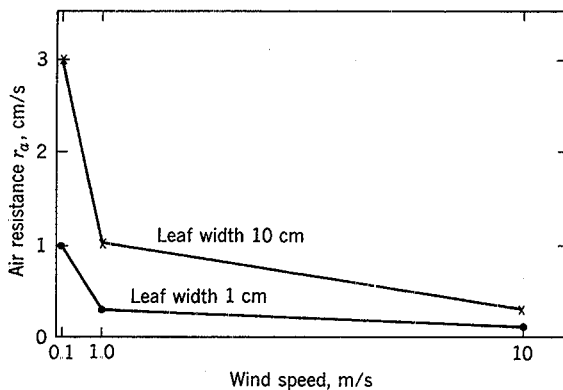
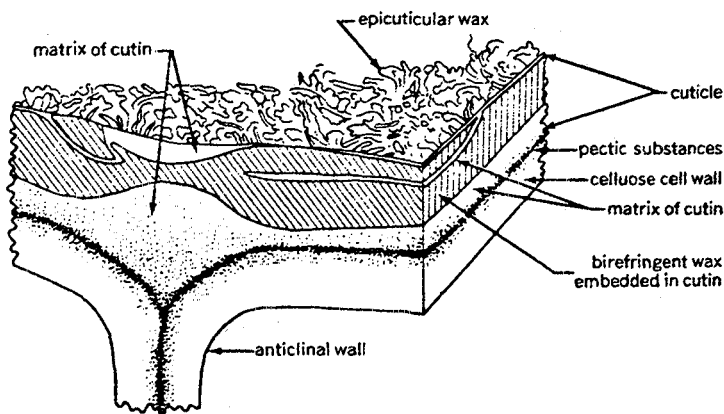


Figure 7.6 Approximate boundary layer resistance at three wind speeds for a cotton leaf 10 cm wide and a grass leaf 1 cm wide. From Kramer (1983), after data of Slatyer (1967).

**Leaf Orientation.** Leaves with surfaces perpendicular to the sun's rays are warmer than those more or less parallel, and are likely to have a higher rate of transpiration. Leaves of many plants tend to be more or less perpendicular to midday radiation, but there are exceptions such as some species of *Lactuca* and *Silphium*, turkey oak (*Q. laevis*), and jojoba (*Simmondsia chinensis*). The leaves of *Stylosanthes humilis* normally are perpendicular to the sun's rays but when the pulvini lose turgor they become parallel. Pine needles that occur in bundles, such as those of the three and five needle pines, shade one another and reduce transpiration and photosynthesis per unit of surface (Kramer and Clark, 1947). Leaf orientation may be less important in stands of plants than in individual plants.

**Leaf Surface Characteristics.** The outer surfaces of leaves, flower petals, stems, and fruits often are covered by a relatively waterproof layer, the cuticle. This is composed of cutin and wax, anchored to the epidermis by a layer of pectin (Fig. 7.7). When dry, the cuticle is relatively impermeable to water, as shown by its high resistance (Table 7.4), but when wet it is fairly permeable to water vapor and a variety of solutes (Schönherr, 1976). The cuticle generally is thinner on shade than on sun leaves, and thinner on leaves grown with adequate water than on leaves subjected to water deficits (Bengston *et al.*, 1978). Cuticle mutants have been found in sorghum, some of which displayed thin cuticles and high water loss through the cuticle (Jenks *et al.*, 1994). Permeability to water must depend more on the amount of wax than on the thickness of the cuticle because cuticular transpiration often increases severalfold when the wax is re-



**Figure 7.7** Diagram of an upper surface of an epidermal cell of pear leaf, showing cuticle, composed of cutin and wax. The cutin is anchored to the cellulose wall by a layer of pectin. From Kramer (1983), after Norris and Bukovac (1968).

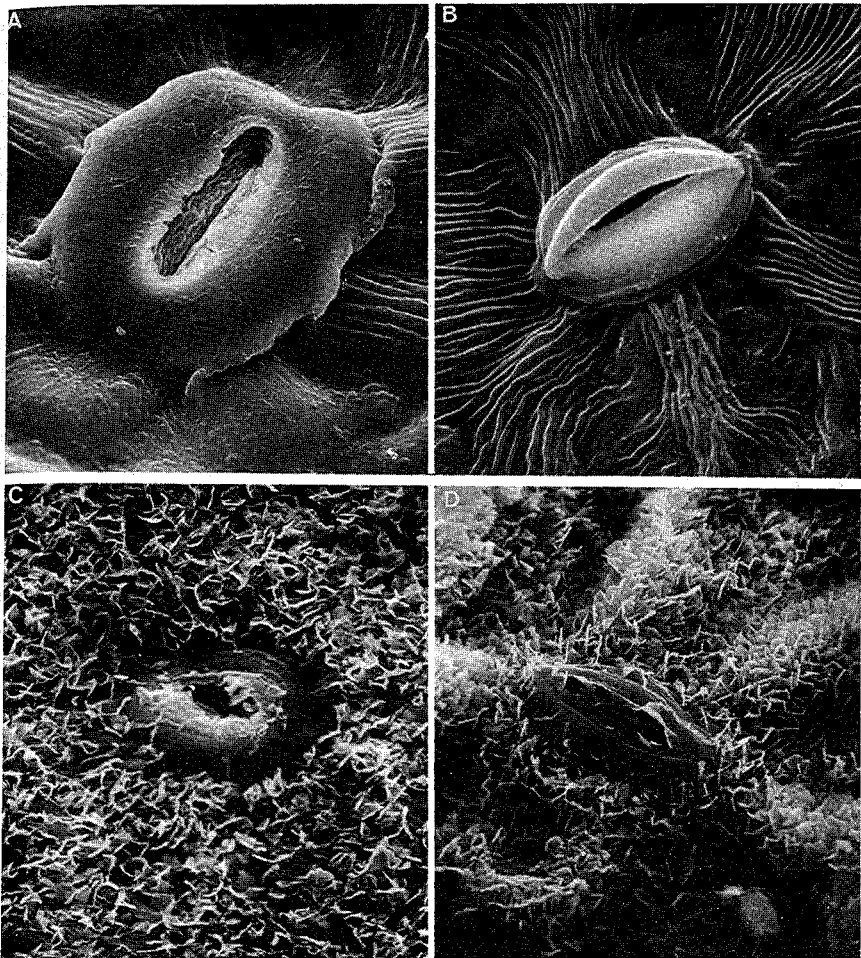


Figure 7.8 Variations in patterns of wax deposited on leaves of four tree species: (A) American elm, (B) white ash, (C) sugar maple, and (D) redbud. Also note differences in appearance of stomata. Photographs by W. J. Davies, from Kramer (1983).

moved (Radler, 1965; Jeffree *et al.*, 1971). However, Chamel *et al.* (1991) claimed that the extraction of soluble lipids did not increase permeability. Examples of wax deposits on leaves are shown in Fig. 7.8. The early work on cuticle was reviewed by Stålfelt (1956b), and Kolattukudy (1981) reviewed the synthesis of cutin and suberin.

Leaves of some plants are covered by thick layers of trichomes or epidermal hairs that reflect light, decrease the driving force by decreasing the leaf tempera-

ture, and increase the boundary layer resistance. Ehleringer (in Turner and Kramer, 1980) studied the role of leaf hairs in the genus *Encelia*. The densely pubescent, white leaves of the desert shrub *E. farinosa* reflect more radiation than the green leaves of *E. californica* which reduces their midday temperature about 5°C below that of coastal *E. californica*. Unfortunately, the hairs reflect so much light that the net photosynthesis of *E. farinosa* also is reduced. Overall, Ehleringer concluded that at high air temperatures the gain in net photosynthesis from a reduced leaf temperature is more valuable than the reduction in transpiration. Although thick coats of hairs may have some adaptive advantages, many desert plants thrive without them while some mesophytes such as mullein (*Verbascum thapsus*) have them, although mullein grows in environments where hairs can scarcely be beneficial. Johnson (1975) concluded that pubescence cannot be regarded as a simple adaptation to arid environments.

Hairs sometimes have other functions unrelated to leaf temperature or transpiration. They often secrete chemicals which give plants characteristic odors and other special properties. For example, Turkish-type tobacco has more aroma than other types of tobacco because of the greater density of secretory hairs on its leaves (Wolf, 1962). Other plants such as nettles sting the skin on contact because of substances produced in hairs on their epidermal cells. Epidermal cells on leaves of some plants develop into glands (Sachs and Novoplansky, 1993).

**Leaf Structure.** Leaf structure is greatly modified by the environment; sun leaves usually are smaller and thicker, with thicker cuticle than shade leaves of the same species, as shown in Fig. 7.9. Van Volkenburgh and Davies (1977) found that leaves of field-grown cotton and soybean were thicker than leaves on plants grown in greenhouses or growth chambers and that cool nights increased the leaf thickness on plants in growth chambers. Patterson *et al.* (1977) also found more mesophyll tissue and a higher rate of photosynthesis per unit of leaf surface in field-grown cotton than in the thinner leaves of cotton grown in growth chambers. The transpiration rate of well-watered *Ilex glabra* and *Gordonia lasianthus*, which have thick, heavily cutinized leaves, is greater per unit of leaf surface in sunny weather than transpiration of oak, maple, and yellow poplar (Table 7.8). Swanson (1943) reported that on sunny days American holly transpired more per unit of leaf surface than lilac, coleus, or tobacco, but on cloudy days when the stomata were closed it transpired less. The ratios of internal to external surface were 12.9, 7.1, and 4.6 to 1.0 for holly, tobacco, and coleus, and a high ratio of internal to external surface provides more internal evaporating surface (Turrell, 1936; Nobel in Turner and Kramer, 1980).

**Stomata.** As mentioned earlier, most of the water lost by plants escapes through the stomata and most of the carbon dioxide used in photosynthesis

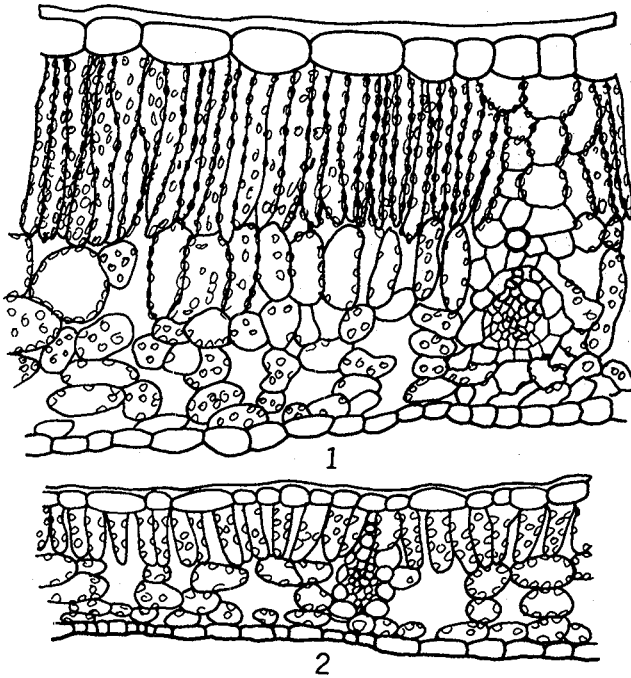


Figure 7.9 Difference in structure of sun leaves from the southern edge (1) and shade leaves from the center of the crown (2) of an isolated sugar maple (*Acer saccharum*). From Kramer (1983), after Weaver and Clements (1938).

enters through them. Thus, stomatal behavior plays a very important role in plant physiology. For example, the cycling in stomatal aperture discussed in Chapter 8 causes cycling in transpiration (Shirazi *et al.*, 1976, and Fig. 8.7). Stomatal behavior is discussed in Chapter 8 and stomatal control of transpiration is discussed by Jarvis and McNaughton (1986).

According to Meinzer and Grantz (1991), an increase in the leaf area of a stand of sugarcane is accompanied by a decrease in stomatal conductance per unit of leaf area, causing transpiration to approach a maximum per unit of ground area instead of increasing linearly with the leaf area. This keeps leaf water status quite constant over a wide range of growing conditions. They suggest that this coordination of canopy conductance with hydraulic conductance may be mediated by chemical regulators of stomata carried from roots to shoots in the transpiration stream (Meinzer *et al.*, 1991).

**Leaf Coatings.** It would be expected that substances leaving a light-colored residue on leaves, such as the Bordeaux mixture, or light-colored dust would

Table 7.8 Midsummer Transpiration Rates of Various Species of Trees<sup>a,b</sup>

Species	Location	Season	Duration (days)	Number of Plants	Average transpiration (g · dm <sup>-2</sup> · day <sup>-1</sup> )
<i>Liriodendron tulipifera</i> <sup>c</sup>	Columbus, OH	August	1	7	10.11
<i>Liriodendron tulipifera</i> <sup>d</sup>	Durham, NC	August	3	4	11.78
<i>Quercus alba</i> <sup>d</sup>	Durham, NC	August	3	4	14.21
<i>Quercus rubra</i> <sup>d</sup>	Durham, NC	August	3	4	12.02
<i>Quercus rubra</i> <sup>e</sup>	Fayette, MO	July	14	6	8.1
<i>Acer saccharum</i> <sup>e</sup>	Fayette, MO	July	14	6	12.2
<i>Acer negundo</i> <sup>e</sup>	Fayette, MO	July	14	6	6.4
<i>Platanus occidentalis</i> <sup>e</sup>	Fayette, MO	July	14	6	8.8
<i>Pinus taeda</i> <sup>d</sup>	Durham, NC	August	3	4	4.65
<i>Clethra alnifolia</i> <sup>d</sup>	Durham, NC	August	3	4	9.73
<i>Ilex glabra</i> <sup>d</sup>	Durham, NC	August	3	4	16.10
<i>Myrica cerifera</i> <sup>d</sup>	Durham, NC	August	3	4	10.80
<i>Gordonia lasianthus</i> <sup>d</sup>	Durham, NC	July	23	4	17.77
<i>Liriodendron tulipifera</i> <sup>f</sup>	Durham, NC	August 26–September 2	12	6	9.76
<i>Quercus rubra</i> <sup>f</sup>	Durham, NC	August 26–September 2	12	6	12.45
<i>Pinus taeda</i> <sup>f</sup>	Durham, NC	August 26–September 2	12	6	5.08

<sup>a</sup>Expressed as grams of water lost per square decimeter of leaf surface per day.

<sup>b</sup>All seedlings were grown in soil near field capacity.

<sup>c</sup>From Meyer (1932).

<sup>d</sup>From Caughy (1945).

<sup>e</sup>From Biswell (1935).

<sup>f</sup>From Kramer (unpublished).

lower leaf temperature and reduce transpiration. In fact, there were early reports that the Bordeaux mixture did reduce water loss, but later studies, summarized in Miller (1938, pp. 465–470), indicate that it causes considerable increases in night-time transpiration. Southwick and Childers (1941) found little effect of the Bordeaux mixture on transpiration of apple leaves, but some reduction in photosynthesis. It was reported by Beasley (1942) that application of light-colored dusts such as talc increased the night transpiration of coleus, but only if applied to the lower leaf surfaces when the stomata were open. This suggests that talc operates by mechanically blocking the stomata open. In recent years interest has shifted to waterproof coatings and substances that cause stomatal closure. These are called antitranspirants and are discussed in Chapter 12.

### Disease

The effects of disease on plant water relations are often neglected, but can be important. According to Durbin (1967), when sporulation begins, transpiration from bean leaves infected with rust increases as much as 50%. Infection of barley leaves with powdery mildew also increases transpiration and increased transpiration is likely to occur when any organism breaks the cuticle. Pathogens that attack roots decrease water and mineral absorption, and various wilt diseases, such as *Fusarium* wilt of tomato, and elm and oak blight are caused by pathogens that block the conducting system. Robb *et al.* (1979) reported that *Verticillium* wilt causes partial blocking of the xylem by tyloses and coating on the inner vessel walls. Vascular diseases often result in reduced transpiration, wilting, and death. Grose and Hainsworth (1992) concluded that infection by *Phytophthora* causes more injury to lupine seedlings by blockage of stem xylem than by injury to roots. Zinc toxicity also causes development of an abnormal coating on the inner walls of xylem vessels that may inhibit water movement (Robb *et al.*, 1980). The interaction of plant water status and plant disease is discussed in Kozlowski (1978) and in Ayres and Boddy (1986).

## MEASUREMENT OF TRANSPIRATION AND EVAPORATION

Thus far transpiration has been discussed in terms of individual leaves or plants that can be studied easily in the laboratory or greenhouse. However, from the ecological and agricultural standpoint the behavior of plants in stands is much more important. Light intensity and air movement decrease with distance downward in plant stands and the important boundary layer resistance is that of the stand rather than that of individual leaves. Thus, the effects of leaf size and shape and stomatal aperture are likely to be less important in the water relations of stands than for isolated plants. Some information on gas fluxes in

stands is given in Nobel (1991, Chapter 9). The effects of evaporation from the soil also can be important in open stands, but it usually decreases as stand density increases (Kaufmann and Kelliher in Lassoie and Hinckley, 1991). The important and difficult problem of extrapolation from individual plants to stands is discussed in several papers in "Tree Physiology," Vol. 9, 1991, by Jarvis and McNaughton (1986), and in a book edited by Ehleringer and Field (1993).

### Measurement of Transpiration of Plants and Leaves

The importance of transpiration in the overall water economy of plants has resulted in numerous measurements by several methods, including gravimetric and volumetric measurements, measurement of water vapor, and the velocity of sap flow. Considerable useful information can be found in Chapter 8 of Pearcy *et al.* (1989). We will first discuss measurements on leaves and individual plants and then turn to measurement of combined losses by evaporation from the soil and transpiration from stands of plants (evapotranspiration).

Measurement of transpiration was reviewed by Crafts *et al.* (1949), Franco and Magalhaes (1965), Slavik (1974), Kaufmann and Kelliher (in Lassoie and Hinckley, 1991), and others, and there has been little change in the basic methods for several decades. The best method depends on the kind and size of plant, the objective and duration of the experiment, and the equipment available.

*Phytometer or Gravimetric Methods.* Most measurements from the time of Hales to the present have been made on plants growing in containers which are weighed at appropriate intervals to detect water loss. The size of the plants is limited by the size of the containers and the capacity of the weighing equipment. Small plants usually are grown in small metal or plastic containers of soil weighing a few hundred grams, but Nutman (1941) measured transpiration of coffee trees in tanks of soil weighing 225 kg with a sensitivity of 25 g. An even larger lysimeter was constructed by Fritschen *et al.* (1973) containing a Douglas-fir tree 28 m in height, growing in a block of soil  $3.7 \times 3.7 \times 1.2$  m. The total weight of the container, soil, and tree was 28,900 kg and the sensitivity of the weighing apparatus was 630 g. Lysimeters were discussed in Chapter 4.

The containers in which plants are grown should be protected from direct sun to prevent overheating, and the ideal arrangement is to have them buried with the tops flush with the surrounding soil in the habitat where they would normally grow. This was done by Biswell (1935) and Holch (1931) in their studies of the transpiration of tree seedlings in sun and shade in Nebraska. The soil surface should be covered to keep out rain and prevent evaporation but if the covers are too tight aeration may become limiting. A good seal is needed around stems to prevent unmeasured wetting of the soil by stem flow. Care must also be taken to prevent soil moisture from becoming limiting, especially as



plants grow larger. In long-term experiments, corrections also need to be made for the increasing fresh weight of rapidly growing plants by harvesting samples of plants occasionally and weighing them. Estimates of transpiration over short periods of time may also involve errors caused by a decrease in water content resulting from the lag of absorption behind transpiration shown in Fig. 6.1. A variation of this method is to grow the plants in nutrient solution and measure the volume or weight of solution removed by the roots during a given period of time. Harris (1971), Kitano and Eguchi (1992a), and Simonneau *et al.* (1993) described apparatus for simultaneously measuring water absorption, transpiration, relative water content, and growth. Some data are presented in Fig. 7.20.

Extrapolation of data from potted plants to plants in the field is questionable, but the phytometer method is useful for comparing plants of various species under the same conditions and for measuring the effects of environmental factors and experimental treatments. The desire to estimate the transpiration of plants too large to be easily accommodated in phytometers and the need for rapid measurements resulted in the development of other methods of measuring or estimating the rate of transpiration.

*Cut-Shoot Method.* This sometimes is called the rapid weighing method and was formerly used extensively because of its convenience and applicability to large plants in the field. Shoots or single leaves are detached and suspended on a special balance as near their original location as possible and the change in weight over time is recorded. Such measurements can last for only a few minutes because the transpiration rate tends to decrease with decreasing leaf water content. Also there often is a transient increase in the transpiration rate a minute or two after detachment, the Iwanoff effect, caused by the sudden increase in stomatal opening after release of tension by detachment from the plant. Furthermore, the detached leaf or stem no longer is in competition with the remainder of the shoot for water. The method was discussed by Franco and Magalhaes (1965), Slavik (1974) and others, but is seldom used today.

Sometimes stems of plants are detached under water and are placed in containers, and water uptake is measured over time. However, water uptake often is reduced by plugging of the cut stem surface with air or debris or by microbial activity and the stem must be recut frequently. Ladefoged (1963) and Roberts (1977) made useful measurements of transpiration of forest trees up to 16 m in height by cutting them off under a stream of water and placing the bases of the trunks in containers of water while their tops were supported in their normal position in the canopy. Knight *et al.* (1981) also measured transpiration of lodgepole pine trees up to 30 cm in diameter by this method. Although absorption slowed after 2 or 3 days, it could be restored by recutting the base of the trunk. Myers *et al.* (1987) reported that cutting Eucalyptus stems under water increased leaf water potential, but decreased leaf conductance.

*Measurement of Water Vapor Loss.* Transpiration can be measured by monitoring the change in humidity of an air stream after it is passed through a container enclosing plant material. The containers usually are made of plastic and vary from tiny cuvettes holding part of a leaf to those enclosing a branch (Kaufmann, 1981) to plastic tents enclosing an entire tree (Decker *et al.*, 1962). Although the method eliminates the errors caused by detaching leaves or branches, it creates a somewhat artificial environment. Differences in leaf and air temperature, humidity, and wind speed inside and outside the chamber can cause important differences in transpiration between the enclosed plants and those in the open. Those errors can be minimized by equipment to control temperature and other factors at the same level within as outside the container (Jarvis and Slatyer, 1966). The cuvettes for single leaves or parts of leaves are essentially porometers, as described in Kramer (1983, pp. 328–330). Kaufmann (1981) and Kaufmann (in Hashimoto *et al.*, 1990) used electronically operated chambers large enough to enclose branches for short intervals to measure leaf conductance and estimate tree canopy transpiration. Larger enclosures can be used to measure evapotranspiration from groups of plants in a stand.

The cobalt chloride method described in Miller (1938, pp. 491–493) measures the escape of water vapor by the time required to produce a given change in color from blue to pink of a piece of filter paper impregnated with cobalt chloride and pressed against the leaf surface. As it replaces the normal leaf environment, rates obtained by this method usually do not agree with those obtained by weighing and are not very useful. Other investigators pressed bottles containing a small amount of  $\text{CaCl}_2$  against the leaf to absorb water vapor, but that method has some of the disadvantages of the cobalt chloride paper method. This method is seldom used today.

*Velocity of Sap Flow.* Several investigators have attempted to estimate the rate of transpiration from measurement of the velocity of sap flow by thermal methods. The technology is discussed later in the section on velocity of sap flow in stems. Decker and Skau (1964) found good agreement between simultaneous measurements of velocity of sap flow and of transpiration. Steinberg *et al.* (1990a) reported that the transpiration rate of 5-year-old pecan trees estimated from their sap flow gauge was similar to measurements made on the same trees in a weighing lysimeter. Granier *et al.* (1990) reported that if correction was made for transpiration from the understory there was good agreement between transpiration of a French maritime pine stand calculated from sap flow and from water vapor flux measurements. Dugas *et al.* (1993) compared estimates of transpiration based on sap flow measured by a thermal method and the injection of deuterium as a tracer, or based on porometer measurements of stomatal conductance, compared with gravimetric measurements on small trees. The difference between gravimetric measurements and heat balance methods was less

than between gravimetric measurements and losses calculated from stomatal conductance or the deuterium tracer method. While sap flow measurements provide good nondestructive estimates, reliable measurements of transpiration require calibration against potted plants or plants in lysimeters. Readers will find additional references in Dye and Olbrich (1993), Dugas *et al.* (1993), and in the section on sap flow later in this chapter. According to McKenney and Rosenberg (1993), different methods of estimating evapotranspiration differ in their response to a change in temperature and other climatic conditions. This needs to be taken into account in predicting the effects of climatic change caused by increasing concentrations of atmospheric  $\text{CO}_2$  on potential evapotranspiration.

**Bases for Calculating Transpiration Rates.** After investigators have settled on a suitable method of measuring transpiration, they must select a method of expressing the rate. Generally, it seems reasonable to express transpiration in terms of leaf surface area, but should it be based on one or both surfaces? We have generally used one surface but use of the stomate-bearing surface seems reasonable. Many European measurements have been expressed as units of water lost per unit of leaf fresh weight, but the fresh weight of leaves varies with time of day, from day to day, and among species. An example of the differences in rates based on fresh weight and on leaf area is shown in Fig. 7.10.

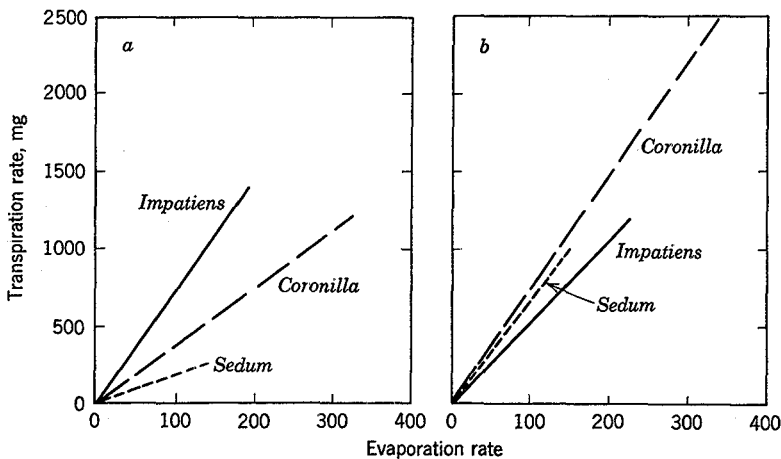


Figure 7.10 Transpiration of three species (*Impatiens noli-tangere*, *Coronilla varia*, and *Sedum maximum*) expressed in (a) milligrams per gram of leaf fresh weight and (b) milligrams per square decimeter of leaf surface. The rate of transpiration is plotted over the rate of evaporation from a filter paper atmometer. The transpiration of *Sedum* varied most with the method used to express it because of its low ratio of surface to mass. Adapted from Pisek and Cartellieri (1932), from Kramer (1983).

Leaf area seems to be the best basis for calculating rates of transpiration and photosynthesis because the receipt of energy is more closely related to the area than to the weight of leaves. However, as mentioned earlier, Nobel (in Turner and Kramer, 1980) pointed out that leaf thickness and the amount of mesophyll tissue can affect the rates of transpiration and photosynthesis per unit of surface area. Use of the leaf area introduces the necessity of measuring or estimating it. If leaves can be separated sufficiently, their area can be measured on a commercial leaf area machine or the area usually can be estimated from a formula relating area to length or width (Wiersma and Bailey, 1975). Sometimes the relationship between area and weight of a representative sample can be obtained and used to estimate the area of a large mass of leaves, such as all of those on a tree, from their weight. Johnson (1984) and Svenson and Davies (1992) discussed methods for measurement of surface area of pine needles, and leaf area measurement is discussed in Lassoie and Hinckley (1991, pp. 466–475).

Transpiration from stems usually is disregarded, but Gračanin (1963) reported that the rate of water loss from the stems of several herbaceous species constitutes a significant fraction of the total water loss. Water loss from large herbaceous stems probably deserves further study. According to Huber (1956), transpiration from the bark of trees is negligible in comparison to leaf transpiration. However, enough water is lost from branches of leafless deciduous trees during sunny winter days to reduce the pressure in the xylem sap and stop maple sap flow by early afternoon.

*Rates of Transpiration.* Despite various errors inherent in the measurement of transpiration, some useful information on daily and seasonal differences and differences among species have been obtained. An example of differences in diurnal rate between a  $C_3$  and a CAM species are shown in Fig. 7.11, and the seasonal course of transpiration of an evergreen and a deciduous species is shown in Fig. 7.12. The evergreen transpiration rate was lower than that of the deciduous tree in the summer, but was higher in the winter because it retained leaves. Table 7.8 shows transpiration rates, measured gravimetrically on potted plants, of a number of woody species measured at different locations. It is somewhat reassuring to find the transpiration rates of well-watered yellow poplar (*Liriodendron tulipifera*) seedlings measured in August at Columbus, Ohio, and Durham, North Carolina, so similar ( $10.11$  and  $11.78 \text{ g dm}^{-2} \text{ day}^{-1}$ ). Also, a comparison of rates of transpiration of six species of European trees measured by two methods, made by four investigators, all indicated that spruce had the lowest rate and birch the highest (Kramer and Kozlowski, 1960, p. 299). Roberts (1983) found that transpiration rates for trees reported from various places in Europe were quite similar, suggesting that the rate of transpiration of European forests is relatively stable and lower than would be expected from potential rates of evaporation.

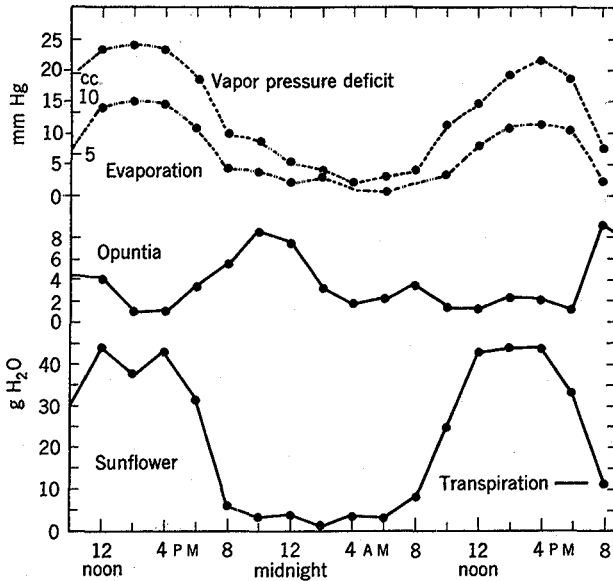


Figure 7.11 Transpiration of sunflower and *Opuntia* plants in soil at field capacity on a hot summer day. The maximum rate of transpiration of *Opuntia* occurred at night, a characteristic of plants with CAM. The early afternoon decrease in the transpiration of sunflower the first day probably resulted from a decrease in turgor and partial closure of stomata. From Kramer (1983), after Kramer (1937).

In contrast, Kaufmann (1985) reported that in the subalpine forests of Colorado there are large differences among tree species. Taking aspen as 1, the ratios of three conifers were lodgepole pine, 1.8; subalpine fir, 2.1; and Engelmann spruce, 3.2. The differences were attributed to differences in leaf conductance,

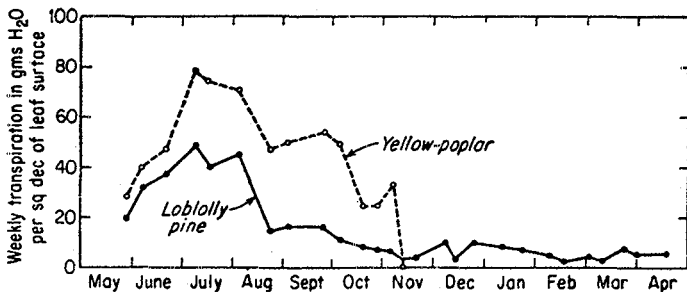


Figure 7.12 Seasonal course of transpiration of potted seedlings of an evergreen and a deciduous species growing outdoors at Durham, North Carolina. From Kramer and Kozlowski (1979).

leaf to air temperature, leaf area index, and the shorter transpiring season of aspen. Such differences have important implications for watershed management.

Roberts (1983) cited studies indicating that moderate variations in soil water content have a negligible effect on forest transpiration. Perhaps this surprising conclusion results from the relatively mild climatic conditions in the British and European forests studied. Low soil moisture certainly often becomes a limiting factor during drought in North America (Lopushinsky and Klock, 1974).

### Evapotranspiration from Stands of Plants

The discussion of transpiration has dealt thus far largely with leaves or individual plants, but plants in nature usually occur in stands or communities and water loss occurs both from the transpiring plants and by evaporation from the surface of the soil in which they are growing, which collectively is known as evapotranspiration (ET). In a stand of plants, transpiration occurs from leaves of various ages and physiological conditions, located at various heights in the canopy and exposed to different microenvironments. Chason *et al.* (1991) discussed methods of estimating the leaf area of forest stands and Baldocchi *et al.* (1991) discussed methods of estimating canopy stomatal conductance. The amount of water lost from the soil by evaporation varies widely, depending on the kind and density of plant cover and thickness of the litter layer.

Jarvis and McNaughton (1986) present an interesting discussion of the problem of scaling up from leaves or plants to stands of plants. The difference in scale results in physiologists emphasizing the importance of stomatal behavior and species differences whereas micrometeorologists emphasize atmospheric conditions measured on a large scale for stands of plants. Problems of scale also are discussed in Ehleringer and Field (1993).

*Measurement of Evapotranspiration.* Measurement of total water loss by evapotranspiration per unit of land surface is more important in agriculture and forestry than measurement of transpiration of individual plants. Such measurements are important for scheduling of irrigation, estimating yields from watersheds, and comparing water use efficiency of various crops. Methods of measuring water loss from land areas include: (1) determination of changes in soil water content, the water balance method; (2) the energy balance method; (3) eddy diffusion, the determination of net upward flow of water vapor from the soil and vegetation; (4) estimates from meteorological data; and (5) the use of lysimeters and catchment basins. The various methods are discussed by Tanner in Hagan *et al.* (1967) and in Kozlowski (1968), by Slatyer (1967, pp. 57–64), by Whitehead and Kelliher (1991b), by Kaufmann and Kelliher (in Lassoie and Hinckley, 1991), and by several authors in Kaufmann and Landsberg (1991).

The water balance method depends on measuring changes in soil water content between rains or irrigations, neglecting or measuring deep drainage beneath the crop or plant stand under study. Measurement of soil water is often made by neutron probes or an array of electrical resistance blocks installed at various depths in the root zone or by time domain reflectometry (see Chapter 4). The most reliable data are obtained from lysimeters located in the plant stand being studied or from stands in catchment basins (Whitehead and Kelliher, 1991b). Measurement of soil water content was discussed in more detail in Chapter 4.

Estimates of water loss by the energy balance method depend on the fact that the amount of water lost from an area of land or water by evaporation depends chiefly on the energy available to evaporate water, the net radiation of Eq. (7.3). Over a period of time of a few days the only important changes are in the heat exchange with the atmosphere and the latent heat used in evaporating water. If net radiation and heat loss are measured the fraction used in evaporating water can be calculated (Slatyer, 1967, pp. 58–59).

*Vapor Flow.* The most direct measurement requires determination of the water vapor flow above a stand of plants, but this requires delicate instrumentation and adequate fetch, and works best on level land. Measurement of the humidity and temperature gradients above the plant stand, and of wind velocity, are necessary to provide data for calculating the vapor flux. Meteorological estimates of evapotranspiration from forest stands have been discussed by Baldocchi *et al.* (1991), Granier *et al.* (1990), Kaufmann and Kelliher (in Lassoie and Hinckley, 1991), and others.

*Empirical Formulae.* Many estimates of evapotranspiration have been made from meteorological observations of such factors as bulk air humidity and temperature, wind speed, and length of day by various workers cited in Kramer (1969, p. 344) and Slatyer (1967, pp. 62–64). The equation developed by Penman and modified by Monteith (1965) is used. Whitehead and Hinckley (1991) and Luxmoore *et al.* (1991) discussed the use of several models and the problem of scaling up from leaves to plant stands.

Jarvis (1985) and Jarvis and McNaughton (1986) discussed the extent to which the transpiration of crops is coupled to atmospheric conditions and termed it the “omega factor,  $\Omega$ .” Tree crops seem to be more strongly coupled to the atmosphere than field crops because they are taller and exposed to more turbulence. If plant stands are closely coupled to atmospheric conditions, porometer data on stomatal conductance can be used to make reliable estimates of transpiration rates.

In full sun, 320 to 380 calories of incident energy per day are available per square centimeter of surface, but 570 calories are required to evaporate a cubic centimeter of water so the maximum possible evapotranspiration is about 6 mm

per day. However, the actual evaporation usually is only about 80% of the theoretical maximum because evaporation also is affected by the vapor pressure gradient and by resistances in the vapor pathway. If evaporation exceeds the calculated potential rate, it often is because incident energy is supplemented by advection, the oasis effect shown in Fig. 7.2. Although the leaf area of plant stands (leaf area index) usually is several times that of the soil on which they grow, water loss cannot exceed that from an equal area of moist soil or a water surface receiving the same amount of energy. As the soil dries, stomatal closure reduces transpiration and drying of the soil surface reduces evaporation from the soil, hence actual ET often is considerably lower than the potential rate calculated from pan evaporation.

Evaporation and transpiration losses from a field of corn and a forest are given in Tables 7.1 and 7.2, and the effect of removing plant cover in increasing runoff and evaporation is shown in Table 7.2. One might expect water losses to be similar from various types of plant cover receiving similar amounts of radiation, but variations in reflectance (albedo), roughness of the canopy, depth of rooting, and stomatal behavior result in significant differences (Rider, 1957). An extreme example is shown in Fig. 7.13. Pineapple is a CAM plant (Joshi

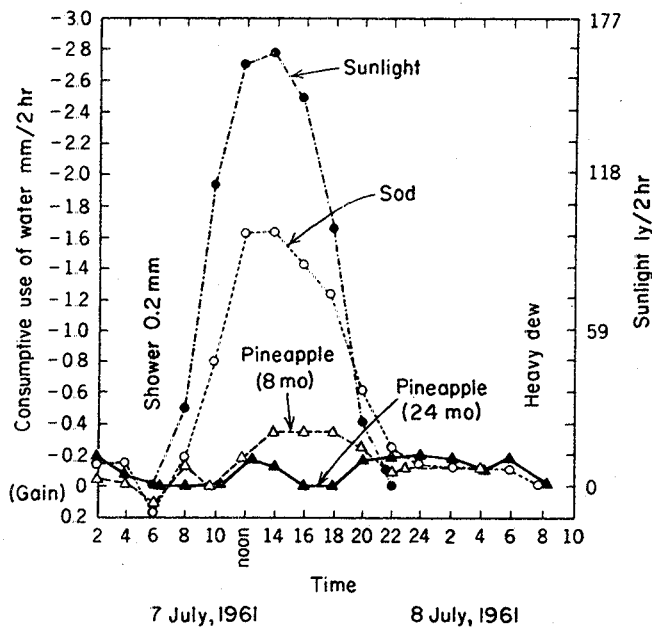


Figure 7.13 Evapotranspiration from a Bermuda grass sod and from stands of pineapple 8 and 24 months after planting. All plants were grown in soil in lysimeters in Hawaii. From Kramer (1983), after Ekern (1965).



*et al.*, 1965) with such a low rate of transpiration that when a mature stand completely shades the ground the rate of evapotranspiration may be lower than that of a younger stand which leaves the soil partly exposed (Ekern, 1965; also see Chapter 12).

Over the entire United States about one-fourth of the total precipitation escapes as stream flow and three-fourths returns to the atmosphere by evapotranspiration from the soil and vegetation. Some precipitation is intercepted and is evaporated directly from the surface of vegetation, but most reaches the soil and is returned either by direct evaporation from the soil surface (49% in an Illinois cornfield, Table 7.1; 45% in a North Carolina deciduous forest, Table 7.2) or by transpiration. The relative losses by evaporation from the soil and from the vegetation are of special interest on watersheds in respect to vegetation management. For example, experiments in humid southwestern North Carolina indicated that conversion from mature, deciduous forest to low growing vegetation increased stream flow 12.5 to 40 cm the first year after cutting; the increase was much greater from north-facing than from south-facing slopes (Hewlett and Hibbert, 1961). According to Bosch and Hewlett (1982) in nearly 100 experiments with catchment basins removal of vegetation always resulted in an increase in runoff. Clear cutting lodgepole pine in Colorado resulted in a 30% increase in stream flow and conversion of chaparral to grass in the central valley of California even doubled runoff. Instances are reported where the removal of forests resulted in a measurable rise in a shallow water table. McNaughton and Jarvis (1983) discussed methods of measuring the effects of vegetation change on transpiration and evaporation, and Kaufmann (1984) developed a canopy model for estimating transpiration of forest stands.

It is fairly common for evapotranspiration to exceed precipitation during the growing season for a year or two, even in an Illinois cornfield, as shown in Table 7.1. The deficit was supplied from stored soil water; the water content of the upper 2.3 m of soil was reduced from 31.0 to 17.7 cm during the growing season. This deficit would be made up during an average winter. An extreme instance was the 18- to 20-year-old apple orchard in eastern Nebraska, studied by Wiggans (1938) during the drought of the 1930s. The trees removed 25 to 38 cm more water per year from the soil than was returned by precipitation, and it was estimated that in 3 more years they would exhaust all the available water to a depth of over 9 m. Presumably the trees eventually would have died from desiccation, but unfortunately they were killed by a severe autumn freeze, prematurely terminating the observations. Many tree plantations in the prairie and Great Plains states flourished for several years on stored soil water, but died when it was exhausted (Bunger and Thomson, 1938).

Another example is the deep-rooted perennial alfalfa, which made excellent growth in virgin soil on stored water in certain areas of Nebraska for the first 3 years, quite independently of current rainfall, after which the yield declined

and became dependent on current rainfall. Alfalfa can absorb water from depths of at least 9 m in well-aerated loess soil, but this water may not be replaced for many years. In fact, Kiesselbach *et al.* (1929) reported that it had not been replaced below 2.0 m after 15 years of crops other than alfalfa.

## THE ASCENT OF SAP

The success and even the survival of land plants depend on sufficient water moving upward from the roots to replace that lost from the shoots by transpiration. The existence of land plants more than a few centimeters in height depended on evolution of an effective water-conducting system because on a hot sunny day the volume lost may exceed the total water content of the plant. Replacement requires an efficient conducting system and a strong driving force in addition to the absorbing system discussed in Chapters 5 and 6. Mosses lack a water-conducting system and are limited in height to a few centimeters. In this section we will first discuss the structure of the water-conducting system, then the driving force that propels water through it.

### The Conducting System

The xylem has been recognized as the principal pathway for the upward movement of water at least since the time of Malpighi and Grew in the 17th century. Anyone can demonstrate this by cutting the stem of a transpiring plant under a dye solution such as acid fuchsin and later making cross sections of the stem above the cut. If the stem is left in dye a few minutes the dye may even become visible in the leaf veins.

There are two kinds of water-conducting elements in xylem: tracheids which are spindle-shaped cells up to 5 mm long and 30  $\mu\text{m}$  in diameter and vessels which are formed by disintegration of end walls of rows of cells, forming tube-like structures ranging from a few centimeters to many meters in length and 20 to 700  $\mu\text{m}$  in diameter. Angiosperm xylem contains both vessels and tracheids, but gymnosperm xylem contains only tracheids. During maturation the proto-plasts of vessel elements die and disintegrate and many of the end walls disintegrate, leaving only the lateral cell walls. The end walls of the remaining xylem elements contain perforations of various shapes through which water flows (Schulte and Castle, 1993, and anatomy texts). Most of the water movement in gymnosperms occurs through tracheids, in angiosperms through vessels, though other types of cells such as xylem parenchyma, and fibers may play a minor role. Movement from one xylem element to another is facilitated by pits or thin places in their walls. Detailed descriptions of vessels and tracheids can be found in anatomy texts, and Zimmermann (1983) discussed xylem structure in relation to water movement. Ewers and Cruiziat (in Lassoie and Hinckley, 1991) also discussed the transport and storage of water in stems.

*Root-Shoot Transition Zone.* There is a change in the arrangement of the conductive tissues in the transition from roots to stems, especially in herbaceous plants. The xylem usually forms a cylinder in the center of roots, but becomes split into a number of vascular bundles arranged in a ring near the outside of stems in most herbaceous plants. Sometimes tissues in the transition zone appear to have special physiological properties. For example, citrus grafted on certain rootstocks are said to be more salt tolerant because  $\text{Cl}^-$  and  $\text{Na}^+$  ions are intercepted in the transition zone (Lloyd *et al.*, 1987; Walker, 1986).

*Woody Plants.* Because of their longer life the conducting systems of woody plants are exposed to greater variations in temperature and water stress than those of herbaceous plants. Because of the greater height of most woody plants they also face special problems. The conducting system often forms a spiral and dye injected near the base of a tree often follows unexpected paths as it moves upward (Kozłowski and Winget, 1963). Thomas (1967) reported that dye in dogwood moves spirally as much as  $90^\circ$  of the circumference per meter of ascent. Rudinsky and Vitè (1959) suggested that a spiral pattern of sap ascent provides a more effective distribution of water to all parts of a tree crown than direct vertical ascent. Kozłowski and Winget (1963) stated that pin oak in which the transpiration stream spreads out in the top suffers more from oak wilt than white oak in which water usually moves straight upward, keeping the fungus more localized.

There seems to be some uncertainty concerning the extent to which particular roots supply particular parts of the shoot. Klepper (in Gregory *et al.*, 1987) stated that in wheat each lateral root usually supplies a particular region of the shoot, but lateral transfer of water and minerals can occur in the xylem. Zimmermann (1983, p. 25) stated that each branch of the crown in trees is supplied with water from many roots, providing a safety factor in case of injury to part of the roots. For example, when Auchter (1923) removed the roots from one side of a peach tree the leaf water content was reduced equally on both sides, indicating free lateral transfer of water in the trunk. Furr and Taylor (1933) also observed free lateral transfer of water in lemon trees irrigated on one side. In view of the interconnections among vascular bundles at nodes in the stems of most herbaceous plants, it seems likely that when the conducting system is damaged, any part of the root system might supply any part of the shoot. However, as indicated in the section on phyllotaxy, considerable resistance to the lateral flow of water may exist.

The stems of woody plants are composed of xylem surrounded by a thin layer of bark containing the phloem and separated from the xylem by the cambium. In young woody plants the wood or xylem consists of sapwood containing many living cells, but as they age those cells begin to die and heartwood forms (Kramer and Kozłowski, 1979, pp. 602–610). Heartwood contains no living cells and is not involved in conduction because the vessels usually have been

blocked by gas bubbles, tyloses, or deposits of gum, resin, and other substances. In older stems most of the cross section is composed of dead heartwood, which usually is darker in color and denser than the sapwood. The lack of essential physiological function in heartwood is indicated by the survival of hollow trees in which it has decayed and disappeared.

Xylem of woody angiosperms may be either ring or diffuse porous. In ring porous species such as ash, oak, and elm the first xylem vessels formed each spring (earlywood) are much larger in diameter than those formed late in the preceding summer (latewood), resulting in a sharp demarcation between successive annual rings. In diffuse porous trees such as birch, maple, and poplar the vessels usually are smaller in diameter, and those formed early in the growing season (earlywood) are nearly the same diameter as those formed at the end of the previous growing season (latewood). The difference between early and latewood enables observers to determine the number of annual rings, and differences in their width indicate the occurrence of droughts and other conditions unfavorable to growth. This relationship led to the development of dendrochronology, the study of the width of rings of old trees and timbers of old buildings, both as an indicator of past rainfall and of age of buildings (Fritts, 1976; Kozlowski *et al.*, 1991, p. 66).

Interest in the conducting system of trees developed long ago. According to Zimmermann (1978), Leonardo da Vinci (d. 1519) wrote that when all branches of a tree are put together they are equal in thickness (area) to the trunk below them. This was developed into the pipe model by Shinozaki *et al.* (1964a,b) who treated the xylem as a collection of tubes. Zimmermann (1978) has an interesting discussion of the varying specific conductivity in various parts of the conducting system, examples of which are shown in Fig. 7.14. The relationship between structure and water movement was reviewed in detail by Fiscus and Kaufmann (in Stewart and Nielsen, 1990) and by Tyree and Ewers (1991), and the structure of woody stems was discussed in Kramer and Kozlowski (1979, pp. 18–38).

In many ring-porous species, water movement is confined to one or a few outer rings because older vessels and tracheids are blocked by air bubbles (embolisms), tyloses caused by extrusion of protoplasts through cell wall pits into the cavities of neighboring cells, and deposits of gum and resin. In diffuse-porous species, several annual rings may function in water movement. The resistance to water flow is much higher in conifer stems where water moves through tracheids with numerous cross walls than in deciduous, broadleaf trees, and the resistance to longitudinal flow is relatively low in vines and roots. The specific conductivity or conductivity per unit of leaf weight in various parts of a birch tree is shown in Fig. 7.14 and the rate of flow in various parts of an oak tree can be seen in Fig. 7.18. According to Tyree and Sperry (1989) the specific conductivity is low in twigs and petioles and the chief resistance to water move-

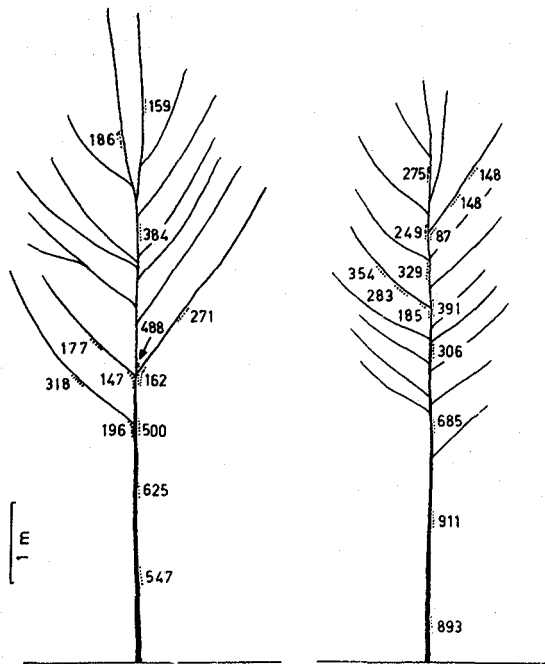


Figure 7.14 Leaf specific conductivity in microliters per hour, per gram fresh weight of leaves supplied, for two paper birch trees (*Betula papyrifera*). Conductivity decreases from lower to upper trunk and in the branches. It also is low when branches are attached to the trunk, as further indicated by the high velocity of sap flow at the point of branch attachment shown in Fig. 7.18. From Kramer (1983), after Zimmermann (1978).

ment is in branches and twigs. It is especially high at the junction of branches with the trunk (Figs. 7.14 and 7.18). It is suggested that growing conditions can modify the conductivity of tree trunks. According to Sellin (1993), the stem xylem of open-grown Norway spruce has greater specific conductivity than that of shade-grown trees because the latter has smaller tracheids and a smaller sapwood area.

**Ratio of Sapwood Area to Leaf Area.** A fairly close relationship exists between the leaf weight or leaf area of trees and the cross-sectional area of the sapwood that supplies the leaves with water, but there are large differences among species. For example, Kaufmann and Troendle (1981) found similar ratios between leaf area and sapwood area in the lower and upper part of the crown in each of the four species they studied. However, there were large differences among the species (see Fig. 7.15), presumably because there are large dif-

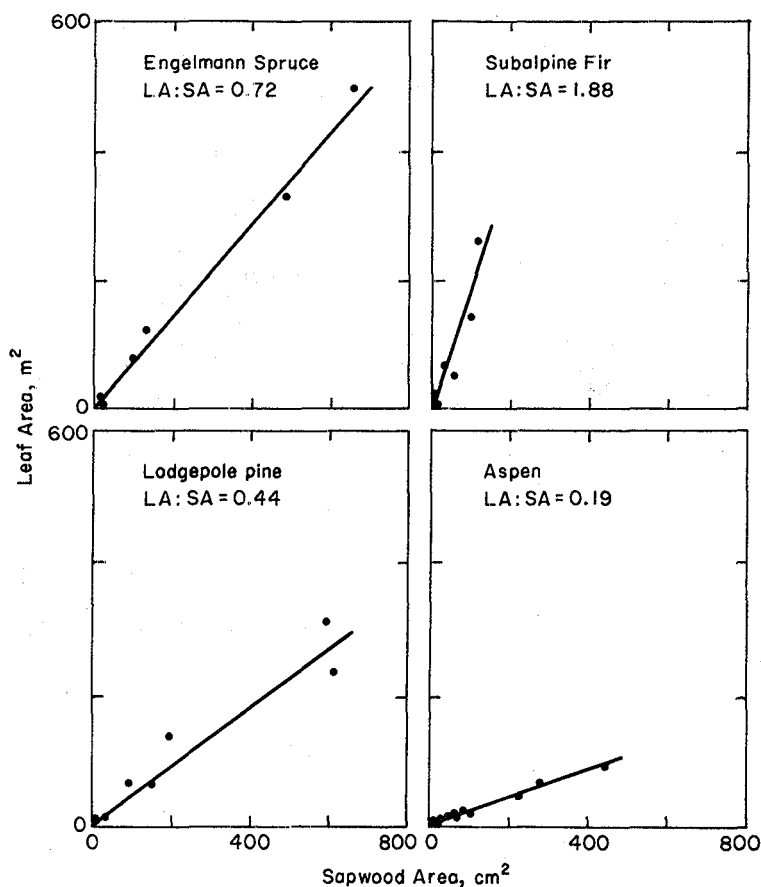


Figure 7.15 Relationship between leaf areas (LA) in square meters and cross-sectional area of sapwood (SA) at 1.37 m above ground for four subalpine forest tree species in Colorado. From Kramer (1983), after Kaufmann and Troendle (1981).

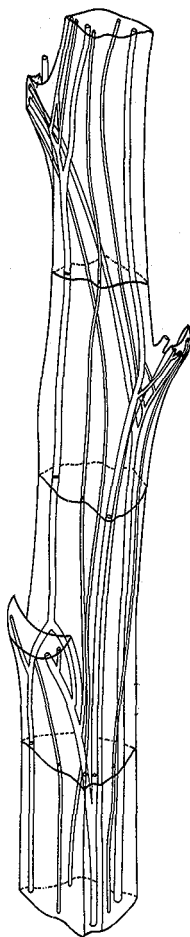
ferences in the efficiency or specific conductivity of their conducting systems. Whitehead *et al.* (1984) also found a linear relationship between leaf area and sapwood cross sections in Sitka spruce and lodgepole pine, but the relationship differed in the two species. No significant difference in the relationship between fertilized and unfertilized trees was found. Gartner (1991) studied the conducting systems of the shrubby and vine forms of *Toxicodendron diversilobum* growing in the same environment. The xylem cross-sectional area per unit of leaf area was smaller in vines, but the sap conductivity was higher in the larger

vessels of vines, resulting in a similar conducting capacity per unit of leaf area in shrubs and vines. Gartner *et al.* (1990) found a higher specific hydraulic conductivity in stems of tropical vines than in trees, but there was much variability within species. A relationship probably exists between leaf area and xylem supplying it in herbaceous plants, but this seems not to have been investigated.

It might seem that the lower resistance to water flow through the large vessels of ring-porous species would be advantageous, but some of the tallest trees in the world are conifers in which water moves through tracheids only a few millimeters in length. Perhaps the shorter, smaller tracheids minimize blockage of the conducting system by decreasing cavitation and the spread of air bubbles as compared with ring-porous species. Thus, a trade-off may exist in which higher resistance to flow through tracheids than vessels is compensated by better protection against blockage and increased resistance later in the season, and both systems are successful.

*Herbaceous Plants.* The conducting system of herbaceous plants often is quite complex, as indicated by the diagram of the branching of vascular bundles at nodes of a potato stem (Fig. 7.16). Because of the numerous interconnections, a local injury does not necessarily produce a serious blockage to water movement (Dimond, 1966). Monocots often have even more complex conducting systems than dicots (Zimmermann and Tomlinson, 1974; Zimmermann, 1978). There is said to be a high resistance to water flow into leaves because of the reduction in number and size of vessels in leaf traces and petioles and there often is a high resistance to flow where branches join the main stem of woody plants, as shown in Figs. 7.14 and 7.18. The water-conducting system of plants is discussed in detail in Chapter 4 of Zimmermann (1983) and by Tyree and Ewers (1991); Black (1979a,b) made a detailed study of resistance to water movement in sunflower.

*Phyllotaxy.* It might be assumed that all leaves on the same side of a stem are supplied with water by the same vascular bundle, but this is not necessarily true. For example, tobacco has 2/5 or 3/8 phyllotaxy, meaning that a vascular bundle supplying leaf 1 goes around the stem twice between leaves 1 and 5 or three times between leaves 1 and 8. Thus, as shown in Fig. 7.17, on a plant with 2/5 phyllotaxy, leaves 4, 5, and 6 are supplied by different vascular strands (Fiscus *et al.*, 1973). Failure to take this into account can lead to misinterpretation of data on leaf water status. Larson (1980) reported that in *Populus deltoides* seedlings the phyllotaxy changes from 1/2 in the cotyledonary stage to 2/5 to 3/8 to 5/13, accompanying increasing leaf production as seedlings grow. In trees with a straight grain, tracers injected at the base rise straight up to leaves above the point of supply but in trees with a spiral grain, tracers may move



**Figure 7.16** Vascular system of a potato stem (*Solanum tuberosum*) showing the complex branching at the nodes. Readers are referred to Dimond (1966) for a study of water flow in tomato stems, which have a similar structure. From Kramer (1983), after Eames and MacDaniels (1947).

around the stem and appear on the side opposite to the injection point. In monocots such as sorghum, maize, and palm trees there is so much interconnection of vascular bundles at lower nodes that a tracer spreads out in all directions.

*Injury to the Conducting System.* There is some uncertainty concerning the amount of injury required to seriously restrict the flow of water to the leaves. Jemison (1944) observed that broad-leaved trees in which the sapwood in over half the circumference near the base of the trunk had been killed by fire made



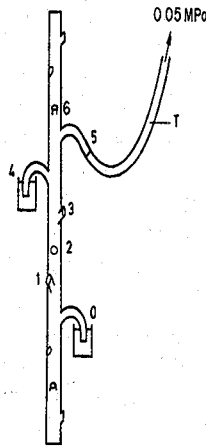


Figure 7.17 Diagram showing leaf attachment on a tobacco plant with 2/5 phyllotaxy. Leaves at positions 0 and 5 are supplied by the same vascular strand whereas leaves at positions 4 and 6 are on different vascular strands. By supplying different dyes to petioles at positions 0 and 4 and removing sap by suction from petiole 5, it was demonstrated that resistance to lateral movement of water from petiole 4 to 5 is much greater than the resistance to longitudinal movement from 0 to 5. From Kramer (1983), after Fiscus *et al.* (1973).

as much growth during the following 10 years as nearby uninjured trees. However, Rundel (1973) reported a strong correlation between fire injury to the base of the trunk and occurrence of dead tops in redwood, a conifer. Postlethwait and Rogers (1958) demonstrated that radioactive phosphorous moved past as many as four horizontal cuts made only 15 cm apart halfway through trunks of pine trees. Thus, it seems that although injury to part of the cross section of woody stems increases resistance to flow, it does not always cause a serious reduction in water and mineral supply to the leaves. Tyree and Sperry (1989, p. 33) suggested that this is possible because the resistance to water flow usually is lower in the main stem than in the branches. Tyree and Sperry (1988) concluded that many water-stressed trees operate near the limit of catastrophic failure when embolisms block part of the xylem, but apparently the limit is seldom exceeded. Yang and Tyree (1993) reported that midday water stress commonly causes a reduction in stomatal conduction and gas exchange of maple leaves, but it is doubtful if excessive stem resistance causes the death of many healthy plants.

Activities of bacteria, fungi, and insects also cause blockage of the xylem. Bark beetles introduce a fungus that blocks water transport in pines and also causes blue stain of the wood. The complex interactions among bark beetles, water stress, and tree physiology were discussed by Lorio (1993). Plugging of the vascular system has often been observed in Dutch elm disease (*Verticillium*

wilt) of elm and maple and in mimosa wilt. In some instances, toxins produced by the fungi stimulate the production of gums which block the xylem. Hsu and Goodman (1978) reported that the bacteria causing fire blight produce a toxin causing rapid wilting of apple, and Suhayda and Goodman (1981) reported that they also produce a high molecular weight polysaccharide that blocks xylem vessels. Thus, injury from vascular wilt disease may have multiple causes (Talboys, 1978; Zimmermann and McDonough, 1978). Experiments of Grose and Hainsworth (1992) suggest that blockage of water conduction in stems can be a more important cause of injury to plants infected with *Phytophthora* than damage to the root system.

Various kinds of stresses, including zinc deficiency and attacks by pathogenic organisms, are said to induce deposits of material on and in walls of xylem vessels (Robb *et al.*, 1980; Van Alfen and Turner, 1975). A later study showed that ABA and *Verticillium* infection cause deposition of suberin on the inner walls of the xylem of tomato and more suberin is produced in resistant than in susceptible cultivars (Robb *et al.*, 1991). The increased suberization presumably hinders the growth of hyphae into adjoining cells and slows spread of the disease, but it must also slow movement of water and solutes through and out of the xylem.

*Blockage by Cavitation.* In rapidly transpiring plants, blockage often occurs by cavitation, the spontaneous rupture of sap columns when subjected to large negative pressure or tension, accompanied by an infiltration of air. The resulting bubbles or emboli are filled with water vapor and air and block the xylem. There is an extensive literature on cavitation, partly because the sound made by its occurrence can be detected with acoustic equipment, making it easy to study. Examples can be found in papers by Milburn and Johnson (1966) and Tyree *et al.* (1984, 1986) and in a review by Tyree and Sperry (1989). Sperry *et al.* (1988a,b) found that in some plants acoustic data did not predict a decrease in hydraulic conductivity accurately because of interference by embolism formation in xylem fibers. Ritman and Milburn (1991) used a combined detector for audible and ultrasound emissions that enabled them to locate sites of cavitation more accurately. Freezing also causes formation of gas bubbles that block xylem elements (Zimmermann, 1964). According to Sperry and Sullivan (1992), freezing produces fewer embolisms in conifers than in nonconiferous trees. The large earlywood vessels of oak are most susceptible to embolism formation, the small vessels of poplar and birch are intermediate, and the tracheids of conifers are least susceptible. Hammel (1967) suggested that the tiny gas bubbles formed in the tracheids of conifers during freezing are reabsorbed during thawing, but it is unlikely that the large bubbles in the larger vessels of ring-porous trees could be removed in this manner. In plants of a few species such as grape and birch, root pressure may aid in refilling gas-filled xylem vessels with

water in the spring (Sperry *et al.*, 1987, 1988a). However, recovery of full capacity to move sap in ring-porous trees probably depends chiefly on production of new xylem each spring (Huber, 1935; Zimmermann, 1964). Tyree *et al.* (1986) concluded that there was enough root pressure in maize, even when water stressed, to refill vessels overnight that have been blocked by cavitation. Borghetti *et al.* (1991) discussed the difficulties in explaining the refilling of embolized tracheids in conifers, and Tyree and Yang (1992) discussed refilling in sugar maple.

One would expect large diameter xylem elements to be more subject to cavitation than elements with a smaller diameter and Dixon *et al.* (1984) found this to be true within a species. However, it is not always true between species, as maple with vessels is less vulnerable to cavitation than cedar and hemlock with only small diameter tracheids. Cochard (1992) reported large differences among species in the xylem water potential required to cause cavitation. Tyree *et al.* (1991) found the stems of the tropical tree *Schefflera morotoni* very susceptible to cavitation, but this was compensated by its large stem capacitance and very high stem conductance per unit of leaf area (leaf specific conductance). Tyree and Sperry (1989) concluded that differences among species in vulnerability to embolism formation depend on differences in the air pressure required to penetrate the intervessel pit membranes instead of on vessel diameter. Cavitation occurs in roots and reduces longitudinal flow (Byrne *et al.*, 1977), and also occurs in cells and may contribute to freezing injury (Ristic and Ashworth, 1993).

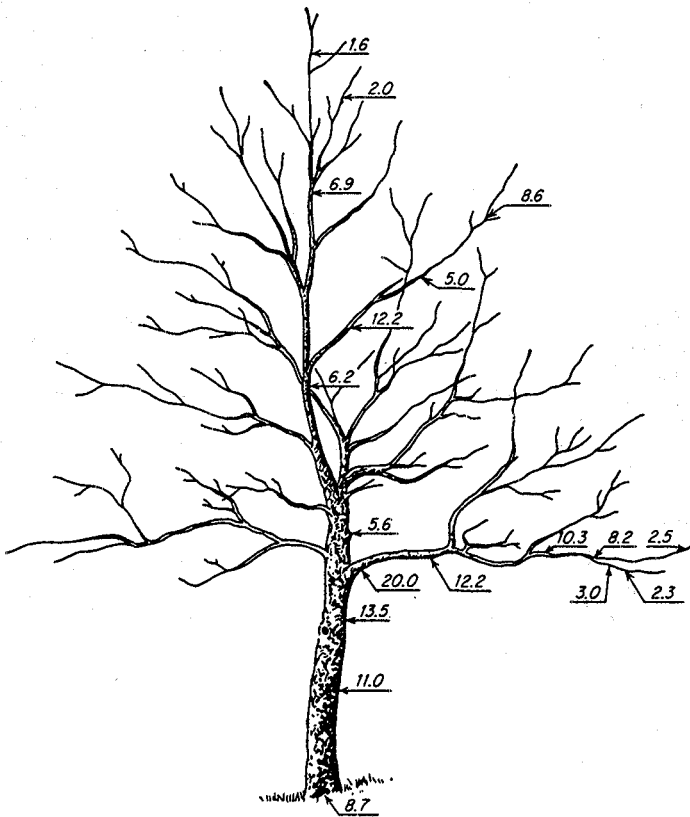
*Velocity of Sap Flow.* Measurements of sap flow velocity have been made by injecting dyes or radioactive tracers (Fraser and Mawson, 1953; Moreland, 1950), but the rate probably is at least temporarily affected by cutting into the stem. The heat pulse method devised by Huber and his colleagues (Huber, 1932; Huber and Schmidt, 1937) and modified by Sakuratani (1981) and others seems to be the most reliable method of measuring the velocity of sap flow because it is noninvasive. Heat is supplied to the sap stream by small electric heating units attached to or embedded in the stem and sap velocity is determined by the time required for warm sap to reach a thermocouple or thermistor placed on the stem above the heater. The theory and inherent problems of this method have been discussed by Marshall (1958), Pickard (1973), Lassoie *et al.* (1977b), Cohen *et al.* (1988), and Groot and King (1992). Cermák and Kučera (1981) and Steinberg *et al.* (1989) developed heat balance methods that compensate for temperature variations in tree trunks and permit more accurate estimation of volume flow than the original heat pulse method. These require temperature measurements at several points relative to the heat source and good insulation of the trunk from external temperature variations. Ham and Heilman (1990) also proposed modifications for high flow rates. Steinberg *et al.* (1990a) re-

ported that transpiration of 5-year-old pecan trees measured with their sap flow gauge was comparable to measurements made on the same trees in a weighing lysimeter. Schulze *et al.* (1985) has an interesting comparison of canopy transpiration and stem flow in conifers, and Lopushinsky (1986) studied daily and seasonal variations in flow rates in conifers. In the spring while the soil was moist the maximum velocity occurred at midday, but late in the growing season, as the soil dried, it occurred earlier in the day. Jones *et al.* (1988b) used the heat pulse method on apple trees and discussed the difficulty in relating it to actual transpiration rates. Dye *et al.* (1992) claimed that the heat pulse and deuterium tracer methods give similar results if care is taken to minimize sources of error, but Cermák *et al.* (1992) claimed that dye injection gives higher velocities than the heat balance method. According to Groot and King (1992), even the latest version of the heat balance method suffers from errors at very low and high rates of sap flow, and Cohen *et al.* (1993) found that the accuracy of both the heat pulse and heat balance methods varied with sap flow velocity.

Sap movement generally starts first in the upper part of trees in the morning and there may be a lag of 2 to 4 hr before sap movement is measurable in the lower part of the stem (Schulze *et al.*, 1985). Steinberg *et al.* (1990a) found sap flow starting simultaneously near the ground and in the upper part of young pecan trees, but this may have resulted from the short transport distance and low capacitance in young trees. In oak and ash the greatest velocities occur near the base, but in birch the rate increases upward, apparently because it has less conducting capacity per unit of leaf area in its slender branches (Fig. 7.14). The rate of conduction in various parts of an oak tree at midday are shown in Fig. 7.18 and rates of movement in stems of various species, measured by various methods, are given in Table 7.9.

Cermák *et al.* (1992) measured water flow velocity at various distances from the periphery in trunks of pedunculate oak and Norway spruce. In oak, velocity was greatest in the youngest annual ring and decreased inward for about 10 rings. In Norway spruce, velocity was greatest in the center of the conducting xylem and decreased toward both the cambium and the heartwood, and variability around the trunk was greater than in oak. According to Granier *et al.* (1990) the rate of water flow is quite uniform at various points across the xylem in Maritime pine.

Another method of measuring water flow in plants is by use of nuclear magnetic resonance imaging. It has been used to measure movement on a scale ranging from less than a millimeter in wheat grains (Jenner *et al.*, 1988) to flow through intact cucumber stems (Van As and Schaafsma, 1984) and leaf petioles (Millard and Chudek, 1993). It appears to be particularly useful for nondestructively measuring changes in water content and water binding in intact plant tissue (Colire *et al.*, 1988; G. A. Johnson *et al.*, 1987; Veres *et al.*, 1991) and for studies of soil-root water exchange (MacFall *et al.*, 1990). Although the



**Figure 7.18** Velocity of sap flow in meters per hour in various parts of an oak tree at midday, measured by the thermoelectric method. The rate of flow decreases toward the top because the relative conducting surface (ratio of xylem cross section to leaf area supplied with water) increases toward the top in oak. In birch (see Fig. 7.14) the relative conducting surface decreases toward the top and the velocity of flow increases. From Kramer (1983), after Huber and Schmidt (1937).

method requires expensive equipment and highly trained technicians, it is developing into a promising tool to study the state of water (bound or free) and its movement in living plant tissue, as well as for morphological studies. Brief descriptions of the technology and some research results are given in Kramer *et al.* (in Hashimoto *et al.*, 1990) and in MacFall and Johnson (1994).

**Direction of Sap Flow.** Water movement generally is upward because transpiration lowers the water potential in the leaves, producing a gradient in driving force in that direction. However, water can move through the xylem in the reverse direction as demonstrated by John Ray in 1669, Hales, and other early

Table 7.9 Rates of Water Movement in Xylem Measured by Various Methods<sup>a</sup>

Investigator	Method	Material	Velocity (m · hr <sup>-1</sup> )
Bloodworth <i>et al.</i> (1956)	Heat pulse	Cotton	0.8–1.1
Greenidge (1958)	Acid fuchsin	<i>Acer saccharum</i>	1.5–4.5
	Acid fuchsin	<i>Ulmus americana</i>	4.3–15.5
Huber and Schmidt (1937)	Heat pulse	Conifers	0.5
	Heat pulse	<i>Liriodendron tulipifera</i>	2.6
	Heat pulse	<i>Quercus pedunculata</i>	43.6
	Heat pulse	<i>Fraxinus excelsior</i>	25.7
Klemm and Klemm (1964)	<sup>32</sup> P	<i>Betula verrucosa</i>	± 3.0
Kuntz and Riker (1955)	<sup>86</sup> Rb	<i>Quercus macrocarpa</i>	27.5–60.0
Moreland (1950)	<sup>32</sup> P	<i>Pinus taeda</i>	1.2
Owston <i>et al.</i> (1972)	<sup>32</sup> P	<i>Pinus contorta</i>	0.1–0.8
Decker and Skau (1964)	Heat pulse	<i>Juniperus osteosperma</i>	0.25

<sup>a</sup>Kramer and Kozlowski (1979).

investigators. Williams (1933) reviewed the early work and demonstrated that enough water will move from leaves immersed in water to keep other leaves on the same plant, but exposed to air, turgid for several days. Daum (1967) demonstrated a reversal of flow in two major branches of an ash tree. Sometimes there was upward flow in the exposed branch and downward flow in the other when it was shaded. Also, after the top was wetted by an afternoon shower there was downward movement toward the roots when they were in dry soil. Occasionally, during periods of plant water deficit, reverse water flow occurs from fruits back into the plant on which they are growing. Lang (1990) observed this in apple and other examples are cited in Kramer (1969, pp. 355–356). Apparently there is no more resistance to water movement in one direction than the other and water moves along the prevailing gradient in water potential. This fact has been used to inject solutions into plants to give unusual flavors to fruits and colors to flowers, remedy mineral deficiencies, and control insects and diseases. The early work was reviewed by Miller (1938, pp. 883–885) and Roach (1934). Baxter and West (1977) reported that injection of water through cut branches of apple trees increased fruit size and Boyle *et al.* (1991b) increased kernel number and size in water-stressed maize by infusion of a culture solution. Rand (1983) discussed movement of water in plants as a problem in biomechanics.

**Capacitance Effects.** Figure 6.1 showed that transpiration often quantitatively exceeds water absorption for much of the daylight period, resulting in transpiration and absorption curves that are out of phase. This phase difference results from what usually is termed the absorption lag. It results in a temporary decrease in the water content of leaves and stems and in the diameter of stems

and thickness of leaves, the size of which depends on the storage capacity (capacitance) of the plant. An example of midday stem shrinkage is shown in Fig. 7.20 and measurement problems are discussed by Neher (1993). Hellkvist *et al.* (1974) published interesting data on vertical gradients of water potential in trees, some of which are shown in Fig. 7.19. For example, when transpiration increases rapidly on a sunny morning the water content and water potential of

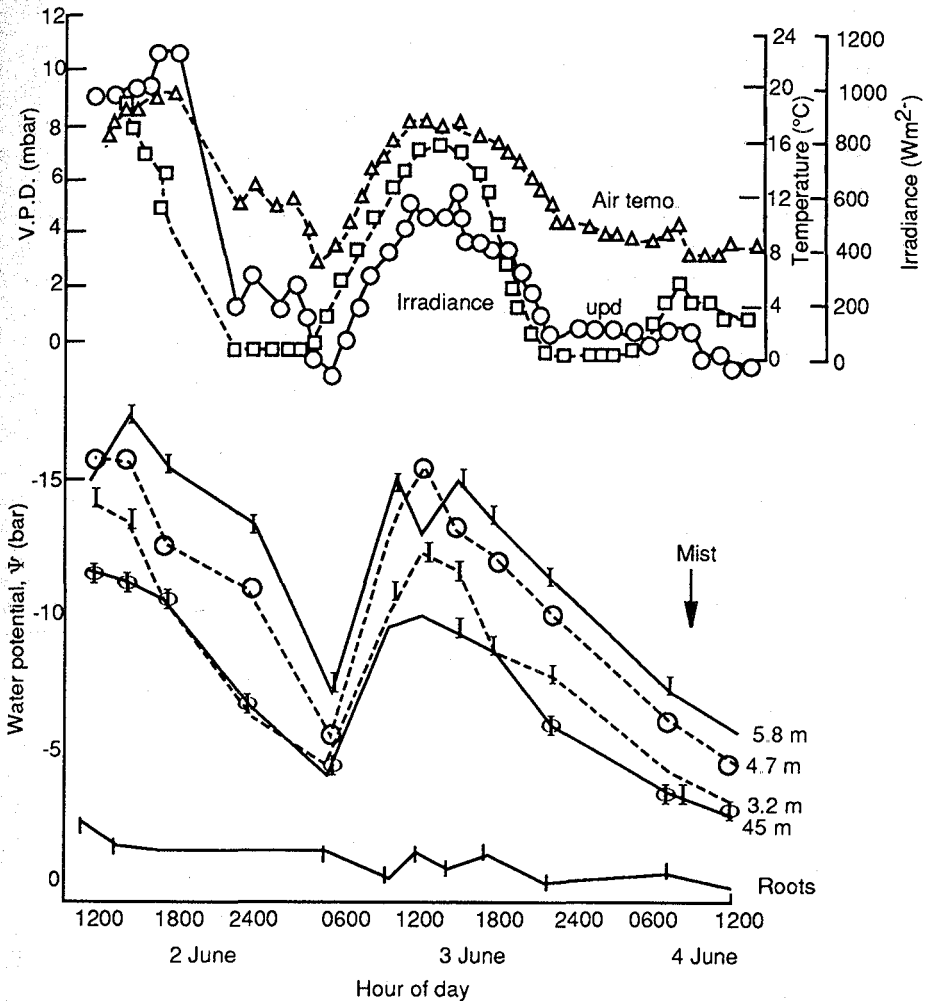
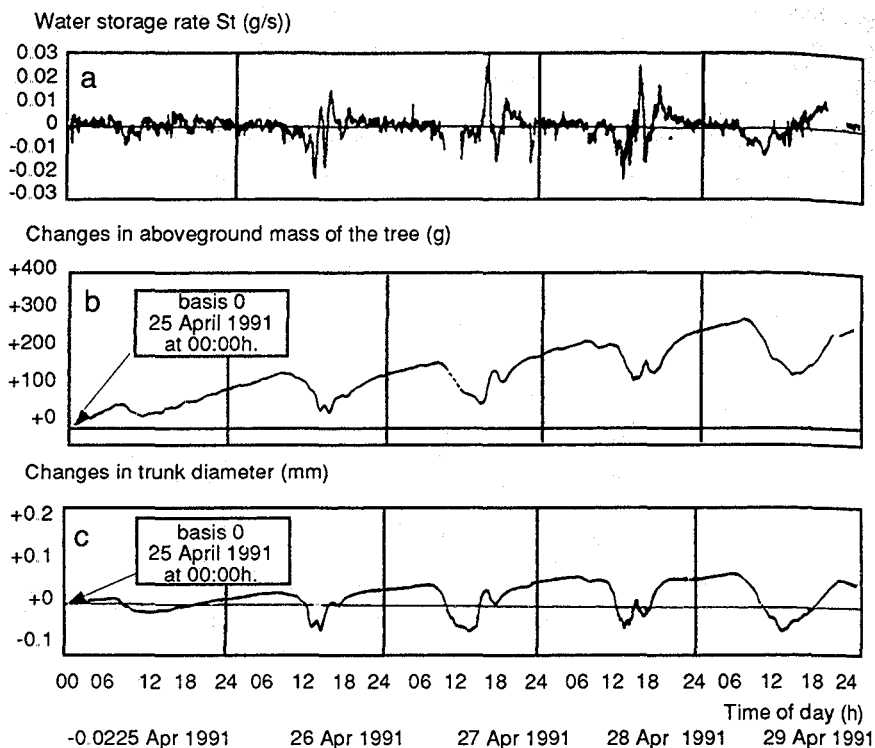


Figure 7.19 Diurnal variation in water potential at four heights on a Sitka spruce tree on a sunny day. The heights are at the point of attachment of the branches on which water potentials were measured with a pressure chamber. From Hellkvist *et al.* (1974), by permission of the authors.



**Figure 7.20** Diurnal changes in water content, stem mass, and stem diameter of a 5-year-old peach tree. (a) Gain or loss in stem water in  $\text{g} \cdot \text{sec}^{-1}$ . Changes in shoot mass (b) and in trunk diameter (c). The first day was cloudy, the others were sunny. Note the good correlation among loss of water, afternoon loss of shoot mass, and stem diameter. From Simonneau *et al.* (1993).

the leaves and upper part of the shoot often decrease and transient wilting may take place. This occurs because the resistance to movement of water out of parenchyma cells is lower than the cumulative resistance to flow of water in from the soil through the roots. If the plants are in moist soil when transpiration slows in the afternoon and evening the parenchyma tissues regain the water lost in the morning. This capacitance effect tends to “dampen” or decrease the severity of midday leaf water deficits in exposed regions of both herbaceous and woody plants. Waring and Running (1978) and Waring *et al.* (1979) claimed that water stored in tree trunks significantly postpones water stress in forest trees, but Carlson and Lynn (1991) found that capacitance had little effect in small plants. Kitano and Eguchi (1993) reported that about 10% of the shoot water content of cucumber was lost by the midday water deficit, causing stomatal closure and a reduction in the rate of leaf expansion.



Simonneau *et al.* (1993) obtained interesting data on transpiration, water absorption, water storage in stems, and changes in stem diameter and mass of 5-year-old peach trees. Some of their data are shown in Fig. 7.20. Nobel (1991, pp. 528–532) discussed the theory of capacitance and it is discussed by Koide *et al.* (in Pearcy *et al.*, 1989). The importance of stored water is discussed in more detail in Chapter 12 in connection with drought tolerance.

### The Mechanism of Sap Rise

The mechanism by which sap rises to the tops of trees has been a subject of speculation for centuries. Root pressure has often been assigned a role, but Hales observed in 1727 that root pressure does not occur in rapidly transpiring plants. Nevertheless, some writers consider its importance to be underestimated (Fensom, 1957; Minshall, 1964) and it probably plays a role in refilling vessels blocked by embolisms (Sperry *et al.*, 1988a,b). During the 19th century several physiologists thought the living cells of stems played an essential role in the ascent of sap, and the Indian physiologist Bose (1923) claimed that sap rise is caused by rhythmic pulsation in root and stem cells. Kargol (1992) developed a hypothesis involving the osmotic activity of living xylem cells to supplement the cohesion theory. However, investigators from Boucherie (1840) and Strasburger (1891) to Kurtzman (1966) have shown that sap will rise through stems or stem segments killed by heat or poisons. Although living cells do not cause the ascent of sap they may be important for the maintenance of favorable conditions by excluding air.

*The Cohesion Theory.* Today it is generally agreed that sap is pulled upward to the transpiring surfaces. This was suggested by Hales (1727), and in the 19th century Sachs and Strasburger concluded that transpiration produces the pull causing the ascent of sap. The cohesion theory became more acceptable when Askenasy (1895) and Dixon and Joly (1895) demonstrated that water confined in tubes has considerable tensile strength and Böhm (1893) demonstrated that transpiring branches can lift mercury above the height to which it is supported by atmospheric pressure.

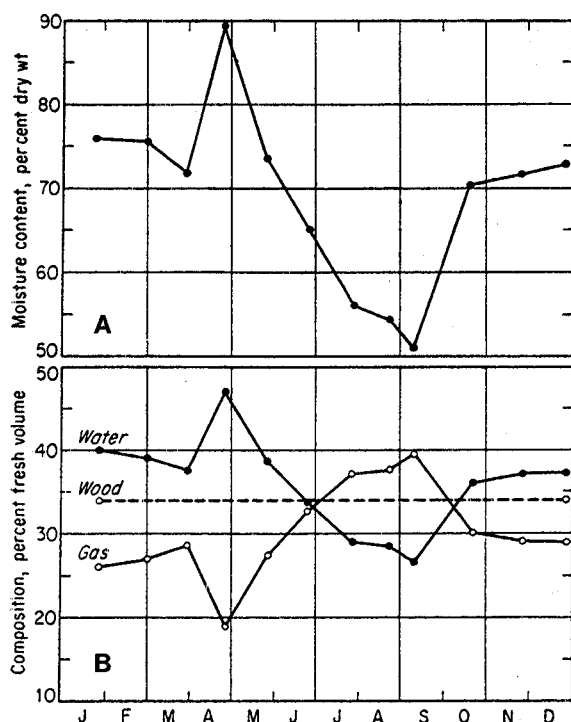
The following are the essential features of the cohesion theory:

1. Water has high cohesive forces and when confined in small tubes such as xylem elements it can be subjected to tensions of many MPa before the columns rupture.
2. Water in plants forms a continuous system through the water-saturated cell walls and xylem elements from the evaporating surfaces in the leaves to the absorbing surfaces of the roots.
3. Evaporation of water from plant cells, chiefly those of leaves, lowers their water potential, causing water to move from the xylem to the evaporating cells

and cell surfaces. This reduces the pressure in the xylem sap and produces a tension or water potential gradient in the cohesive hydraulic system of the plant.

4. This tension is transmitted to the roots where it causes an inflow of water from the soil. Thus, in transpiring plants in moist soil, water absorption is controlled by transpiration, modified only by the lag caused by water stored in plant tissue (capacitance) which sometimes results in absorption lagging an hour or more behind transpiration.

*Problems with the Cohesion Theory.* There was some reluctance among physiologists to accept the cohesion theory (Greenidge, 1957, 1958; Preston, 1961, for example). This was based partly on the instability of water under tension and partly on the blocking of xylem elements by gas embolisms (cavitation). Blockage by gas bubbles (embolisms) formed by cavitation seems to be the principal problem. A large decrease in the water content of many tree trunks exists during the summer, as shown in Fig. 7.21. As mentioned earlier, Tyree



**Figure 7.21** (a) Seasonal change in water content of yellow birch tree trunks calculated from disks cut from the base, middle, and top of the trunks. (b) Changes in gas and water content of yellow birch tree trunks calculated as a percentage of total volume. From Kramer (1983), after Clark and Gibbs (1957).

and Sperry (1988) claim trees often operate near the limit of their conducting capacity because of cavitation, but survival after wounding by experiments and accidents suggest that most trees have considerable excess conducting capacity and it seems that blockage by cavitation rarely is lethal.

Other objections to the cohesion theory of the ascent of sap have appeared. Direct measurement, of the negative pressure in the xylem sap with pressure probes by Balling and Zimmermann (1990) and others indicate that they are lower than those obtained by the Scholander pressure chamber method and are too low to support the cohesion theory. The significance of the new data is discussed by Zimmermann *et al.* (1993), who concluded that several processes are involved in the ascent of sap. These include capillary and interfacial forces, and what they term Maragoni convection which is related to the presence of tiny gas bubbles on the walls of the xylem vessels. Apparently in their view, tension is important only at high rates of transpiration. This has caused some controversy (Passioura, 1991; Zimmermann *et al.*, 1991) and a full treatment would require more space than is available. The main difficulty is that the pressure probe must penetrate the xylem water column while it is under tension, which may disrupt the tension. Thus, there probably are as many errors in measurements with pressure probes as with Scholander pressure chambers. More data are needed before final conclusions can be reached. Furthermore, we emphasize the statement of Renner (1912) that plant survival depends on coordination between rates of water absorption and transpiration, and this can best be accomplished by a continuous sap stream connecting the absorbing and transpiring surfaces. At least for the present, the cohesion theory is regarded as the best explanation of the ascent of sap.

## CONDUCTION IN LEAVES

At each node a branch of the vascular system, the leaf trace, extends out into the leaf. In most conifers a single vein extends the length of the leaf. In grasses, numerous small veins extend more or less parallel to the midvein to the edges of the leaves, where they often anastomose. Those veins are connected by numerous veinlets extending across the mesophyll tissue which they supply with water. The phloem in the veins also provides the means of removing carbohydrate from the photosynthetic tissue. Altus and Canny (1985) have an interesting discussion of the complex venation of wheat leaves. Some dicots have palmate venation in which a few large veins extend out from the base of the leaf blade and are connected by a complex system of smaller veins. Other dicot leaves are pinnately veined, with numerous small veins extending outward on each side of the midrib. Veins usually extend to the tips of lobes and teeth, and Wilson *et al.* (1991) observed that tracers accumulate quickly in the hydathodes of teeth of transpiring balsam poplar leaves. They suggested that hydathodes retrieve solutes from the transpiration stream. In many species, leaf xylem elements

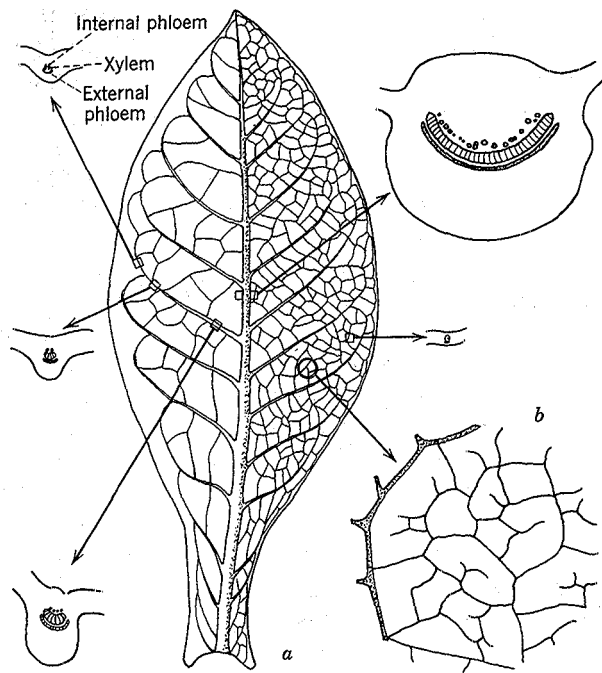


Figure 7.22 (a) Diagrams of venation of a mature tobacco leaf, showing midrib and principal lateral veins, also cross sections of midvein and lateral veins of various sizes. (b) Enlargement of a small section of a leaf blade to show the network of small veins. There were 543 mm of veins per square centimeter on this leaf. From Kramer (1983), after Avery (1933).

branch, rebranch, and reconnect to form a complex network, as shown in Fig. 7.22. As a result, most cells of a leaf are only a few cells away from a vein. Most leaves have so much excess conductive capacity that they often survive injury to major veins (Plymale and Wylie, 1944).

There is some question concerning the pathway by which water is supplied to the epidermal cells. LaRue (1930) and Williams (1950) pointed out that the epidermis in some kinds of leaves is or can be detached from the underlying mesophyll without injury and must be supplied with water from main veins. In some leaves, bundle sheath extensions reach the epidermis and provide a pathway for movement of water and solutes to the epidermis. It has even been suggested that it might be easier for water to move to the epidermis through bundle sheath extensions and then back to mesophyll cells than to move laterally through the mesophyll cells (Wylie, 1943), but this is speculative. There also is a question in leaves, as in roots, concerning the importance of apoplastic versus

symplastic movement of water across masses of cells (Boyer, 1985, pp. 480–483). Canny (1990) reviewed some of the literature on use of tracers to follow water movement in leaves and other tissues and warned that water movement does not always coincide with apparent solute movement. As mentioned earlier, developments in technology such as NMR spectroscopy and imaging, and pressure probe measurements may aid in answering these questions.

## USE OF XYLEM SAP BY PARASITES

Thus far, we have dealt with the role of the xylem in supplying water and solutes to the shoots of plants. However, there are many parasitic plants and some insects that depend on xylem sap for water, minerals, and organic substances. Over 3000 species of angiosperms are said to be fully or partly parasitic; the dodders and mistletoes are the best known. These plants are connected to their hosts by specialized tissues known as haustoria. The haustoria form close contact with the host tissue, but there usually is no direct connection between the xylem of host and parasite except in some mistletoe species (e.g., Sallé, 1983). The transpiration rate of at least some parasitic plants is higher than that of their hosts because their stomata remain at least partly open at night. This probably aids in maintaining the water potential gradient necessary to move water from host to parasite.

A number of different kinds of insects, including cicadas and spittle bugs, use xylem sap, although others such as aphids use phloem sap. Aphids can be employed to sample phloem sap by excising their stylets, which penetrate individual sieve elements, and collecting the exudate (Fischer and Frame, 1984). In contrast to most parasitic plants, insects that penetrate the xylem with their stylets establish direct access to the xylem sap. They filter out solutes and secrete large quantities of water in droplets from the anus. Sometimes these insects spread viruses and bacterial diseases. Much information on sap-feeding organisms has been summarized by Press and Whittaker (1993) and Raven (1983).

## SUMMARY

This chapter deals with the loss of water by transpiration and the movement of water from roots to the transpiring surfaces of shoots, which may vary from a few centimeters to over 100 m above the soil surface. Transpiration refers to the loss of water from plants in the form of vapor and it largely controls plant water status. In warm sunny climates, plants often lose hundreds of times their fresh weight of water during a growing season and several hundred grams of water often are lost per gram of dry matter produced. Transpiration can be regarded as an unavoidable evil, unavoidable because a leaf structure favorable

for the uptake of the  $\text{CO}_2$  required for photosynthesis is unavoidably favorable for the loss of water vapor, and evil because it often causes injury and death to plants by dehydration.

Transpiration chiefly involves the evaporation of water from cell surfaces into intercellular spaces and its diffusion out of plant tissue, chiefly through stomata, and to a lesser extent through epidermal cells of leaves and lenticels in the bark. The rate of transpiration depends chiefly on the supply of water to the evaporating surfaces, the supply of energy to vaporize water, and the resistances in the vapor pathway. The driving force is the difference in vapor pressure between the evaporating surfaces and the outside air, which varies with temperature and absolute humidity. The chief resistances are the stomatal and cuticular resistance of leaves and the boundary or air layer resistance around leaves which varies with leaf size and wind velocity. Stomatal resistance is most important because most water escapes from plants through open stomata.

Measurement of water loss from plants by transpiration and by evaporation from the soil in which they grow, collectively known as evapotranspiration, is useful in comparing the water use efficiency of different kinds of plants, for scheduling irrigation, and for studying the effect of plant cover on yield from watersheds. Most measurements of water loss from individual plants involve gravimetric measurement of plants in pots or in lysimeters, or by frequent measurements of changes in soil water content. Measurements also are made by enclosing leaves or twigs in containers and measuring the change in humidity of a stream of air passed through the container. Measurements of loss in weight of detached leaves are not very reliable, but some success has been attained in estimating the rate of transpiration from the velocity of the sap stream measured by a thermoelectric method.

Measurement of water loss or evaporation from stands of plants is more difficult, but very important. It is estimated from measurement of the soil water balance or the energy balance, or from the humidity gradient above the stand, or is calculated from meteorological data. It can be measured more directly with plants in lysimeters or in small catchment basins.

Replenishment of the water lost from shoots by transpiration requires an efficient water conducting system and it was only after evolution of the xylem that land plants could grow more than a few centimeters in height. In herbaceous plants the xylem occurs in vascular bundles that are interconnected and spiral upward in complex patterns so that one leaf is often supplied from a different xylem strand than that above or below it. In woody plants the xylem forms most of the stem but only a few outer rings of the sapwood usually function in conduction. Water ascent in the heartwood is reduced by gum deposits, tyloses, and gas bubbles. Xylem conduction sometimes is blocked by activities of bacteria, fungi, and insects, and frequently by cavitation, the development of gas bubbles in the lumens of the xylem elements.

There has been debate for centuries concerning the mechanism by which water reaches the tops of trees. However, it is generally agreed that it is pulled up by the matric forces developed in the evaporating surfaces and transmitted to the roots through the cohesive water columns in the xylem. Although the cohesion theory is under attack, it appears to be the best explanation available. The minimum tension developed in the sap stream is about equal to that required to overcome the force of gravity on a column of water twice the height of the plant. The velocity of sap flow varies with the rate of transpiration and the conductive capacity of the xylem and is much greater in woody vines than in trees. A good correlation also exists between the cross-sectional area of sapwood and the leaf area supplied, although there are wide variations in the ratio among species. The greatest velocity of sap flow usually occurs near midday and movement is slowest at night and on cloudy and rainy days. Downward movement of water can occur as readily as upward movement if the driving force is reversed.

There is some uncertainty concerning the path water follows through masses of living cells such as the root cortex and mesophyll parenchyma of leaves. In such tissues it is difficult to determine how much water moves through protoplasts (the symplast) and how much through cell walls (the apoplast). Use of modern technology such as the pressure probe and nuclear magnetic resonance may help to solve this problem.

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