

Leaf Anatomy and Leaf Elasticity

In this chapter we learn how to measure leaf elasticity and calculate moduli of elasticity for the leaves. But before we study elasticity, we need to look at leaf anatomy to understand the type of organ for which we are making the calculations.

23.1 LEAF ANATOMY

Plants are usually classified according to their water relations as follows: xerophytes, mesophytes, and hydrophytes (Esau, 1977; p. 351). Xerophytes are adapted to dry habitats. Mesophytes require abundant available soil water and a relatively humid atmosphere. Hydrophytes (or hygrophytes) depend on a large supply of moisture or grow partly or completely submerged in water. The structural features typical of plants of the different habitats are referred to as xeromorphic, mesomorphic, and hydromorphic, respectively. The characteristics that distinguish plants of the various habitats are most striking in leaves. Here we consider dicotyledonous and monocotyledonous leaves and focus mainly on mesophytes, and then we look at special adaptations of xerophytes.

23.1.1 Dicotyledonous Leaves

Figure 23.1 shows a dicotyledonous leaf. It is a leaf of the shrub, lilac (*Syringa vulgaris* L.) (Torres and Costello, 1963; p. 124). It is composed of an upper (adaxial) and lower (abaxial) epidermis. One stoma is evident in the lower epidermis. The thin, colorless layer deposited on the walls of the upper epidermal cells is called the cuticle and is composed of a waxy material called cutin (Torres and Costello, 1963; p. 43). The mesophyll is divided into an upper palisade mesophyll and a lower spongy mesophyll. One or two layers of columnar, compact cells lie beneath the upper epidermis. These cells make up the palisade mesophyll (also called the palisade parenchyma). Between the palisade tissue and the lower

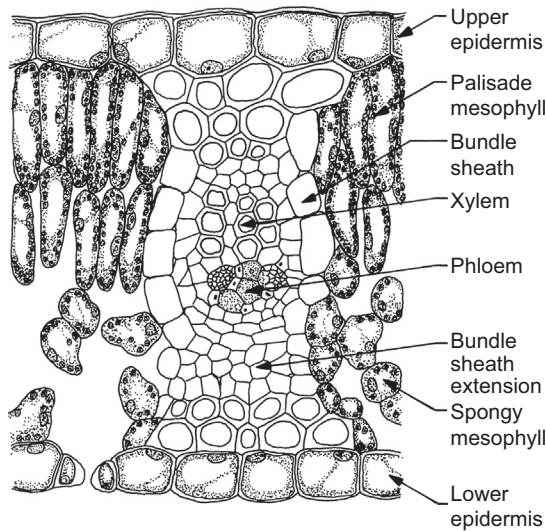


FIGURE 23.1 A transverse section of a lilac leaf, a dicotyledonous leaf. From *Torres and Costello (1963)*, p. 124. This material is reproduced with permission of The McGraw-Hill Companies.

epidermis, there is a layer of large, irregular, loosely packed cells with many intercellular spaces between them. This tissue is the spongy mesophyll (also called the spongy parenchyma). The stoma in [Figure 23.1](#) is located near the intercellular spaces, which allows easy transport of carbon dioxide to the mesophyll. Chloroplasts, oval-shaped bodies, are present in the mesophyll cells. Dispersed throughout the mesophyll are the veins of the leaf. A vein is a strand of vascular tissue in a flat organ such as a leaf ([Esau, 1977](#); p. 531). The largest central vein is known as the midrib. The vein is in the center of [Figure 23.1](#), and the conducting tissue of the vein consists of xylem and phloem. The xylem tissue is closest to the adaxial surface, because, when the vascular tissue bends over from the stem into the leaf, the xylem, which is closer to the center of the plant in each vascular bundle than the phloem (see Chapter 17, Section 17.1, for stem anatomy), comes out on top of the vascular bundle. Thus, the xylem is on top of the phloem in the leaf vascular bundle. In the figure, the cells in the xylem are shown with thick walls and are empty because the vessel members are dead at maturity. A bundle sheath surrounds the vascular tissue. The bundle sheath extensions link the bundle sheath to both the upper and lower epidermis. The bundle sheath extensions have thick cell walls because they are made up of sclerenchyma.

In the dicotyledons, the supporting tissue in leaves may be collenchyma or sclerenchyma, which we defined in Chapter 17, Section 17.1. In the collenchyma tissue only one type of cell is identified, a collenchyma cell. It is living tissue closely related to parenchyma. In fact, it is usually

regarded as a form of parenchyma specialized as supporting tissue in young organs (Esau, 1977; p. 4). The sclerenchyma tissue has two types of cells: sclereids and fibers. Both types of cells have thick, secondary, often lignified cell walls and may lack protoplasts at maturity. The sclereids vary in shape from polyhedral to elongated and may be much branched. Fibers are generally long, slender cells (Esau, 1977; p. 4) with a lignified or nonlignified secondary wall. A fiber cell may or may not have a living protoplast at maturity (Esau, 1977; p. 510). Sometimes it is hard to distinguish fibers and sclereids, so a third type of sclerenchyma cell is identified as a fiber sclereid, which is a sclerenchyma cell with characteristics intermediate between those of a fiber and a sclereid (Esau, 1977; p. 510). The vascular bundles themselves also contribute to the support of the blades. The collenchyma occurs along the larger veins, on one or both sides. Sclerenchyma occurs in the form of bundle sheaths and bundle sheath extensions, composed of fibrous cells, and as sclereids in the mesophyll.

Many herbaceous dicotyledons have leaves with a relatively undifferentiated mesophyll (Esau, 1977; pp. 355–357). The palisade tissue is absent or weakly developed, the intercellular volume is large, and the leaf is often thin. The epidermis bears a thin cuticle, and the stomata are more or less raised. Examples of leaves with relatively undifferentiated mesophyll are those of *Pisum sativum* (pea) and *Lactuca sativa* (lettuce). A thin, loosely organized mesophyll with a single row of palisade cells is found in *Raphanus sativus* (radish), *Solanum tuberosum* (potato), and *Lycopersicon esculentum* (tomato). Leaves of the species *Gossypium* (cotton) have long palisade cells that occupy approximately one-third to one-half of the blade thickness.

Various shrubby and woody species furnish examples of leaves with well-differentiated palisade parenchyma on the adaxial side of the leaf (e.g., *Vitis*, grape; *Syringa*, lilac, Figure 23.1; *Ligustrum*, privet; and *Pyrus*, pear) (Esau, 1977; pp. 356–357).

23.1.2 Monocotylendous Leaves

The leaves of the monocotyledons vary in form and structure, and some resemble those of the dicotyledons (Esau, 1977; p. 359). Monocotyledonous leaves may have petioles and blades, for example *Canna* (common name is also canna) and *Hosta* (plantain lily). But the majority is differentiated into blade and sheath, and the blade is relatively narrow. The venation is typically parallel. In contrast, dicotyledonous leaves normally show a reticulate pattern of venation (Bowes, 2000; p. 10).

The anatomic structure of monocotyledonous leaves ranges from hydromorphic to extreme xeromorphic. Hydrophytes in the monocotyledons show the same basic features as those in the dicotyledons, and

both have an abundance of aerenchyma. Aerenchyma is parenchyma tissue containing particularly large intercellular spaces of schizogenous, lysigenous, or rhexigenous origin. *Schizogenous* is a term applied to an intercellular space originating by separation of cell walls along the middle lamella (Esau, 1977; p. 524), *lysigenous* is a term applied to an intercellular space originating by the dissolution of cells (Esau, 1977; p. 514), and *rhexigenous* is a term applied to an intercellular space originating by the rupture of cells (Esau, 1977; p. 524).

Numerous monocotyledonous leaves develop large amounts of sclerenchyma, which in some species serves as an important source of commercial hard leaf fibers. The fibers are associated with the vascular bundles or appear as independent strands (Esau, 1977; p. 360).

The grass leaf typically consists of a more or less narrow blade and a sheath enclosing the stem. Vascular bundles of different sizes alternate rather regularly with one another, as typified by the wheat leaf (Figure 23.2). The median bundle may be the largest (Esau, 1977; p. 360). The mesophyll of grasses shows, as a rule, no distinct differentiation into palisade and spongy mesophyll (parenchyma), although sometimes the cell rows beneath both epidermal layers are more regularly arranged than in the rest of the mesophyll. In some grasses, the mesophyll cells surround the vascular bundles in an orderly manner, each cell oriented with its longer diameter at right angles to the bundle so that in transverse sections the mesophyll cells appear to radiate from the bundles (Esau, 1977; p. 360).

The epidermis of grasses contains a variety of cells. The narrow guard cells of the stomata are associated with subsidiary cells (see Chapter 24,

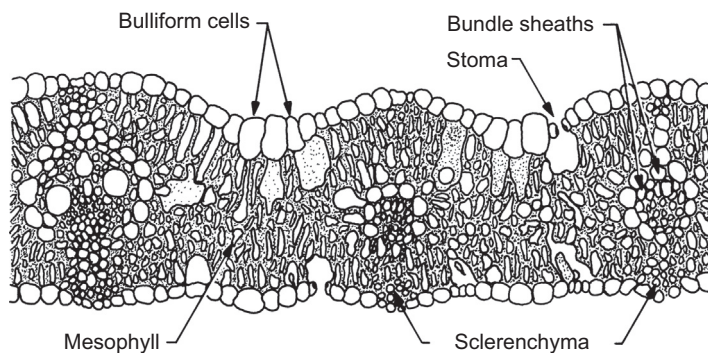


FIGURE 23.2 A transverse section of a wheat leaf, a monocotyledonous leaf. The adaxial epidermis bears bulliform cells in grooved parts of the blade. Subepidermal cells are elongated like palisade cells. There is an inner thick-walled and an outer thin-walled bundle sheath. Sclerenchyma in the ribs is connected with the bundle sheath. From Esau (1965), p. 700. This material is used by permission of John Wiley & Sons, Inc.

Section 24.2, for stomatal anatomy). Silica cells, cork cells, and trichomes may be present. Enlarged epidermal cells, referred to as *bulliform cells* (Figure 23.2), are cells participating in folding movements of grass leaves. In a number of xeric grasses, enlarged epidermal cells line adaxial grooves between the vein ribs and are continuous with similarly enlarged mesophyll cells, called the *hinge cells*. During excessive loss of water, the bulliform cells or the hinge cells, or both, become flaccid and enable the leaf to fold or to roll. But the shrinkage of the various large, thin-walled cells is only one factor causing folding, because leaves without such cells also respond to loss of moisture by rolling. Differential shrinkage of other tissues, distribution of sclerenchyma, and cohesive forces among tissues also contribute to rolling and folding of leaves (Esau, 1977; p. 362).

Grass leaves have strongly developed sclerenchyma. Commonly, fibers extend from the large vascular bundles to the epidermis. The leaf margins may have fibers, as do leaves of wheat (not shown in Figure 23.2 because the figure shows only the center of the leaf; but see Figure 19.8C in Esau (1977), p. 363, for the sclerenchyma at the edge of a wheat leaf).

23.1.3 Grass Leaf Structure and Type of Photosynthesis

The bundle sheaths of grasses show variations that are significant taxonomically and indicators of the type of photosynthesis characteristic of the species (Esau, 1977; p. 362). After the discovery of the C_4 or Hatch and Slack (1966) pathway of photosynthesis in sugarcane [see Laetsch (1974) for a review of the history of the discovery of the C_4 photosynthetic pathway], comparative grass leaf anatomy became the object of intensive investigation in relation to photosynthesis (Esau, 1977; p. 364).

The most common photosynthetic cycle is the C_3 or Calvin–Benson pathway. In C_3 plants, carbon dioxide from the atmosphere is fixed as phosphoglyceric acid, a three-carbon compound. In C_4 plants, an additional mechanism is involved, in which atmospheric carbon dioxide is fixed as oxaloacetic acid, a four-carbon molecule. The leaves of C_3 and C_4 plants differ in morphology as well as in the chemical mechanisms of carbon dioxide fixation (Mellor and Jensen, 1986). In C_3 plants, chloroplasts are found in mesophyll cells throughout the leaf cross-sections. Bundle sheath cells that surround the vascular bundles in C_3 plants are lacking or essentially lacking in chloroplasts.

In leaves of C_4 plants, such as corn leaves, however, the chloroplasts that fix carbon dioxide by the C_3 mechanism are highly concentrated in the bundle sheath cells. In a C_4 leaf, the chloroplasts that fix carbon dioxide by the C_4 mechanism are located in the relatively large mesophyll cells that make up the body of the leaf. The four-carbon malic and

aspartic acids (formed from the initial four-carbon product, oxaloacetic acid) produced by the chloroplasts in these mesophyll cells are transported to the C_3 chloroplasts in the bundle sheaths. Enzymes there split off carbon dioxide from the malic and aspartic acids, and this carbon dioxide is taken up by the C_3 mechanism to form phosphoglyceric acid, the compound that is metabolized to produce the various carbohydrates, proteins, and other compounds that make up the major components of the plant. The three-carbon molecule left after the splitting of carbon dioxide from malic and aspartic acid is pyruvic acid. The pyruvic acid is returned to the C_4 chloroplasts, where it is activated by transfer of a high-energy phosphate group from adenosine triphosphate to form phosphoenolpyruvate. The phosphoenolpyruvate in turn reacts with incoming carbon dioxide from the atmosphere to form oxaloacetic acid, with the loss of phosphate. This completes the C_4 cycle. Thus, in C_4 plants there are two connected carbon dioxide fixing cycles. The C_4 cycle feeds the C_3 cycle (Mellor and Jensen, 1986).

The C_4 cycle is characteristic of plants that require relatively high temperatures for growth. In the angiosperms, this cycle has been recorded in representatives of some 18 families, including the grass family, Poaceae (Ehleringer et al., 1991). This number is few compared to the total number of plant families, which is about 300 (Kirkham, 2011; p. 252). The C_4 plants are widely distributed in the various evolutionary arms of the angiosperms and are among the most recently evolved (Hatch, 1992). About half of the species of Poaceae are included among the C_4 plants (Esau, 1977; p. 364). The C_4 plants are of tropical origin and occur widely in xerophytic environments. In northern regions, few angiosperms are specialized for the C_4 photosynthetic cycle. Woolhouse (1978) shows a map with the percentage distribution of C_4 grasses in the flora of North America. In far northern regions of Canada and Alaska, 0% of the flora has the C_4 photosynthetic pathway; in the southern United States, high percentages occur (e.g., 80% in southern Florida).

23.1.4 Xerophytic Adaptations

Plants overcome adverse conditions of a particular environment in different ways (Esau, 1977; p. 351). In a habitat deficient in water, for example, some plants develop features protecting the aerial parts from excessive loss of water; others form underground water storage organs, or develop roots reaching great depths [e.g., the deep roots of sunflower; see Rachidi et al. (1993), who found depletion of water by sunflower roots at the 2.7 m depth]; and still others control the problem by having a short life span restricted to the time when water supply is most abundant. Availability of water is an especially important factor affecting the

form and structure of plant leaves. Xeromorphic characteristics of leaves include:

1. Thick cuticle (wax)
2. Small intercellular spaces
3. A large proportion of mechanical tissue (sclereids, fibers)
4. Relatively small cells
5. Multiple epidermis
6. Several layers of palisade cells between the epidermis and the spongy parenchyma
7. Sunken stomata
8. Presence of hairs in stomatal pits (crypts)
9. Ledges of wall material on upper and lower sides of guard cells (appears as horns)
10. Presence of water storage cells
11. Spines
12. Lignified cells

[Fahn and Cutler \(1992\)](#) survey morphological and anatomical adaptations that enable plants to grow in arid and semiarid regions.

23.2 INTERNAL WATER RELATIONS

Plants have little storage capacity for water compared with the amounts that pass through them each day ([Baver et al., 1972](#); p. 394). They must regulate their water status to survive. To understand this regulatory process, we must discuss the internal water balance of plants, including elasticity. Here we look at leaf elasticity from a physical point of view. We follow the analysis of [Gardner and Ehlig \(1965\)](#), which also has been partially reproduced in [Baver et al. \(1972, pp. 394–398\)](#).

As we saw in Eqn (17.1), under equilibrium conditions the state of the water in plant leaf cells may be written in terms of the various components of the potential energy, as follows

$$\Psi = \Psi_s + \Psi_p + \Psi_m + \Psi_g, \quad (23.1)$$

where Ψ is the total water potential, Ψ_s is the osmotic (solute) potential component, Ψ_p is the pressure potential component (turgor pressure), Ψ_m is the component due to adsorption forces such as those in the cell wall, and Ψ_g is the component due to gravity. We usually ignore gravity, so [Eqn \(23.1\)](#) becomes

$$\Psi = \Psi_s + \Psi_p + \Psi_m, \quad (23.1a)$$

The partition of energy between the osmotic and adsorption components is somewhat arbitrary, because some of the water in the leaf tissue may be subject to both osmotic effects and adsorption forces, particularly at low leaf-water content. In the vacuole, the osmotic component is important.

If the cell solution were to behave ideally, the osmotic pressure would be directly proportional to the solute concentration (i.e., van't Hoff's law, which we discussed in Chapter 17, applies). There would exist, then, a simple relation between osmotic potential and cell water content:

$$\Psi_s = \Psi_s^o / \theta, \quad (23.2)$$

where Ψ_s^o is the osmotic pressure at full turgor and θ is the relative water content of the cell. θ is the ratio of the water content of the cell to the water content that it has when in equilibrium with free water at the same temperature and pressure. If the amount of bound water is appreciable, then this amount should be subtracted from θ . Some investigators have found appreciable amounts of bound water (as much as 30%; Slavík, 1963). However, we shall consider the amount of bound water to be small, and we shall not subtract it from θ .

The osmotic and pressure components of the potential are not independent. Because of the elastic nature of the cell wall, changes in turgor pressure cause changes in cell volume, due to changes in cell water content. An increase in the turgor pressure results in an expansion of the cell walls. This is accomplished by the uptake of water. Unless this uptake is also accompanied by a proportional uptake of solutes, the solute concentration decreases with a consequent increase in the osmotic potential. Solute transport across the membranes can and does occur, but at a rate that is generally slower than the rate of water movement, so that the immediate response of a cell to any change in water potential is a change in its water content or degree of hydration (Baver et al., 1972; p. 396).

As stated, the components of the water potential in a leaf cell are not completely independent. On a short-term basis, if the total water potential is specified, this determines both the osmotic and the turgor potential, as well as the degree of hydration. (We recognize that we can never *measure* zero water potential in a leaf, even when fully hydrated. The water potential is always slightly negative.)

As the relative water content decreases, the solute concentration must increase proportionately, if the solute content remains constant (Gardner and Ehlig, 1965). This results in a decrease in the osmotic potential. If it is assumed that the relation between the turgor pressure and the cell volume is linear, then

$$\Psi_p = e(\theta - \theta_0) / \theta_0, \quad (23.3)$$

where θ_o is the relative water content at which the turgor potential becomes zero and e is the modulus of elasticity. Substituting Eqns (23.2) and (23.3) into Eqn (23.1a), we get

$$\Psi = \Psi_s^o / \theta + e(\theta - \theta_o) / \theta_o + \Psi_m(\theta), \quad (23.4)$$

in which Ψ_m is now a function of θ . Equation (23.4) gives us a relation between the water potential and the relative water content of the cell. $\Psi_m(\theta)$ represents the relation between the water content and the matric potential. Growth can be expected to cause some departure from the expression used in deriving Eqn (23.4), but to the extent that the assumptions are valid, Eqn (23.4) gives a unique relation between the total water potential and the relative water content of the leaf.

In practice, it is easier to make the measurements needed to test Eqn (23.4) on tissue rather than on single cells. Therefore, Gardner and Ehlig (1965) used tissue [leaves of cotton (*Gossypium hirsutum* L.), bell pepper (*Capsicum frutescens* L.), sunflower (*Helianthus annuus* L.), and birdsfoot trefoil (*Lotus corniculatus* L.)]. The plants were grown in a greenhouse. To obtain different values of water potential, they withheld water from the plants until their leaves wilted to the desired extent. Water potential and osmotic potential were determined with thermocouple psychrometers. The relative water content was determined by using the method of Barrs and Weatherley (1962).

Figure 23.3 shows the relation between the relative water content and osmotic potential for the four plant species, as determined by Gardner and Ehlig (1965). The data are plotted on a logarithmic scale and the straight line has a slope of 45°, as would be predicted if the solute content were to remain constant and the amount of bound water were negligible.

If a plant is growing in a saline soil solution, then over a period of time, the solute content of the cells tends to adjust accordingly. The rate of adjustment varies from species to species. Figure 23.4 shows the relation between the total water potential and the osmotic potential for bell pepper on both saline and nonsaline substrates (Ehlig et al., 1968).

If we neglect the matric and gravitational potentials, we can use Eqn (23.1) to obtain the turgor potential by subtracting the osmotic potential from the total water potential. All three potentials are plotted as a function of relative water content for nonsaline plants (Figure 23.5). Of particular interest is the abrupt change in slope of the pressure potential (turgor potential) at a leaf relative water content of about 0.85. In pepper, for example, this corresponds to a total water potential of about -11 bars (-1.1 MPa) and coincides with the appearance of marked symptoms of visible wilting. The change in slope corresponds to a change in the elastic modulus of the leaf tissue and explains the wilting symptoms. This also corresponds roughly with the point at which the stomata are almost completely closed (Baver et al., 1972, p. 398).

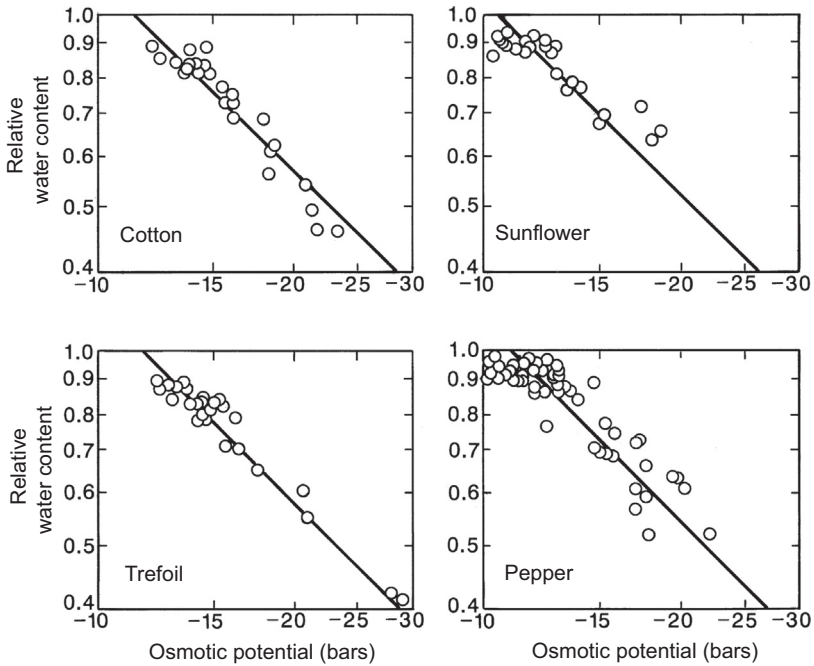


FIGURE 23.3 Leaf relative water content as a function of the average osmotic potential in the plant leaf. The straight lines represent the relation expected if the solutes behave ideally and there is no bound water. From [Gardner and Ehlig \(1965\)](#), *American Society of Plant Physiologists*. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.

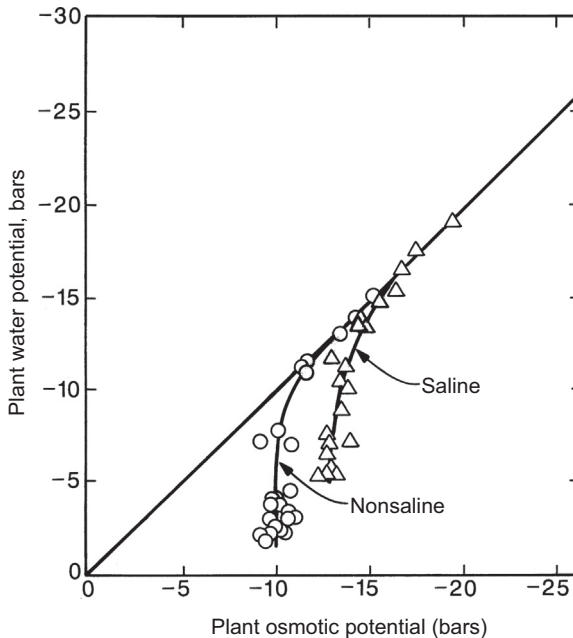


FIGURE 23.4 Plant leaf-water potential (total) as a function of the osmotic potential component. From [Ehlig et al. \(1968\)](#), *American Society of Agronomy: Madison, Wisconsin*. Reprinted by permission of the American Society of Agronomy.

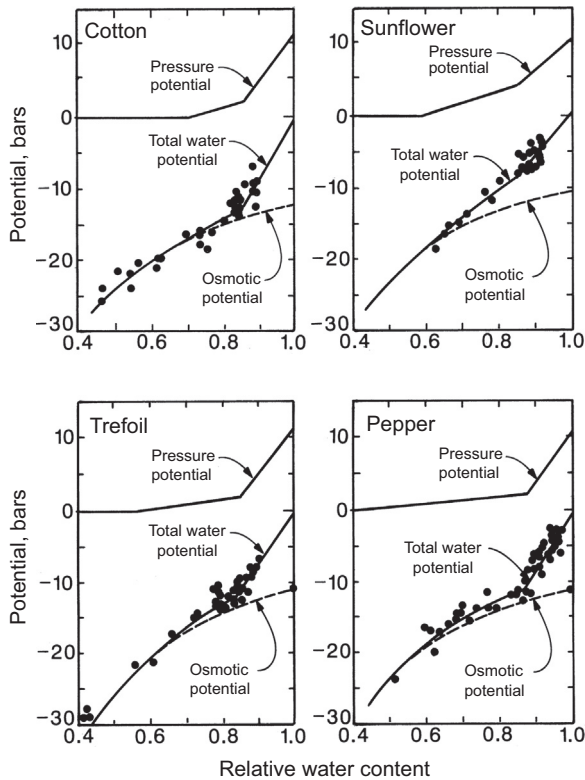


FIGURE 23.5 The osmotic, pressure, and total water potential of the plant leaf as a function of the relative water content. The circles represent the experimentally determined values for the total water potential. The dashed line is the theoretically predicted osmotic potential. The osmotic and pressure potential components are added to give the calculated relation between total water potential and relative water content indicated by the smooth curve. From [Gardner and Ehlig \(1965\)](#), *American Society of Plant Physiologists*. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.

23.3 ELASTICITY

Before we look at the data that [Gardner and Ehlig \(1965\)](#) calculated for the moduli of elasticity of the plants they studied, let us define *modulus of elasticity*. To do this, we refer to a college physics book ([Schaum, 1961](#); pp. 90–91). *Elasticity* is defined as the property by virtue of which a body tends to return to its original size or shape after a deformation and when the deforming forces have been removed. *Stress* is measured by the force applied per unit area that produces or tends to

produce deformation in a body. It is expressed in such units as lb/ft², newton/m², and dyn/cm².

$$\text{Stress} = \text{force}/(\text{area of surface on which force acts}) = F/A. \quad (23.5)$$

Strain is the fractional deformation resulting from a stress. It is measured by the ratio of the change in some dimension of the body to the total value of the dimension in which the change occurred (strain is a pure number and has no dimensions). Thus, if a wire of initial length l experiences an elongation Δl when a force is applied to the wire, the *longitudinal strain* is

$$\text{longitudinal strain} = (\text{change in length})/(\text{initial length}) = \Delta l/l. \quad (23.6)$$

The *elastic limit* is the smallest value of the stress required to produce permanent strain in the body. Within the elastic limit of any body, the ratio of the stress to the strain produced is a constant. This constant is called the *modulus of elasticity* of the material of the body.

$$\begin{aligned} \text{Modulus of elasticity} &= \text{stress required to produce unit strain} \\ &= \text{stress/strain} \end{aligned} \quad (23.7)$$

[Equation 23.7](#) is called *Hooke's law*. (For a biography of Hooke, see the Appendix, [Section 23.5](#).)

There are two types of elasticity: length elasticity and volume elasticity. We now define *length elasticity* or *Young's modulus*, Y . (For a biography of Young, see the Appendix, [Section 23.6](#).) Consider that a wire or rod of length l and cross-sectional area A experiences an elongation Δl when a stretching force f is applied to it. Then

$$\begin{aligned} Y &= (\text{longitudinal stress})/(\text{longitudinal strain}) = (F/A)/(\Delta l/l) \\ &= (Fl)/(A\Delta l) \end{aligned} \quad (23.8)$$

Y may be expressed in lb/in², newton/m², or dyn/cm². Y depends only on the material of the wire or rod and not on its dimensions.

We now define *volume elasticity* or *bulk modulus*, B . Consider that a body is subjected to a hydrostatic pressure, the same amount of force acting perpendicularly on each unit of surface area. The shape of the body remains the same but its volume decreases.

$$\begin{aligned} \text{Volume stress} &= F/A = \text{normal force per unit area} \\ &= \text{pressure increase } \Delta p \end{aligned} \quad (23.9)$$

$$\text{Volume strain} = (\text{volume decrease } \Delta V)/(\text{initial volume } V) = \Delta V/V \quad (23.10)$$

$$B = \text{volume stress/volume strain} = \Delta p/(\Delta V/V) = (V\Delta p)/\Delta V \quad (23.11)$$

The reciprocal of the bulk modulus of a substance is called the *compressibility* of the substance.

23.4 ELASTICITY APPLIED TO PLANT LEAVES

Now let us return to the analysis of [Gardner and Ehlig \(1965\)](#). They wanted to determine the elasticity of plant cells. They first plotted turgor potential (pressure potential) versus relative water content ([Figure 23.6](#)). If the relative water content is taken as a measure of average cell size (volume) (i.e., they are calculating bulk modulus), it is obvious that cell size is not a simple linear function of turgor pressure. However, the data can be represented reasonably well by two straight line segments. One of the line segments is drawn so as to pass through the point of maximum turgor pressure corresponding to Ψ_s^0 , as determined from [Figure 23.3](#), when $\theta = 1$. It appears that Hooke's law is obeyed reasonably well, if a distinction is made between a condition of high turgor pressure and one of low turgor pressure and with a different (bulk)

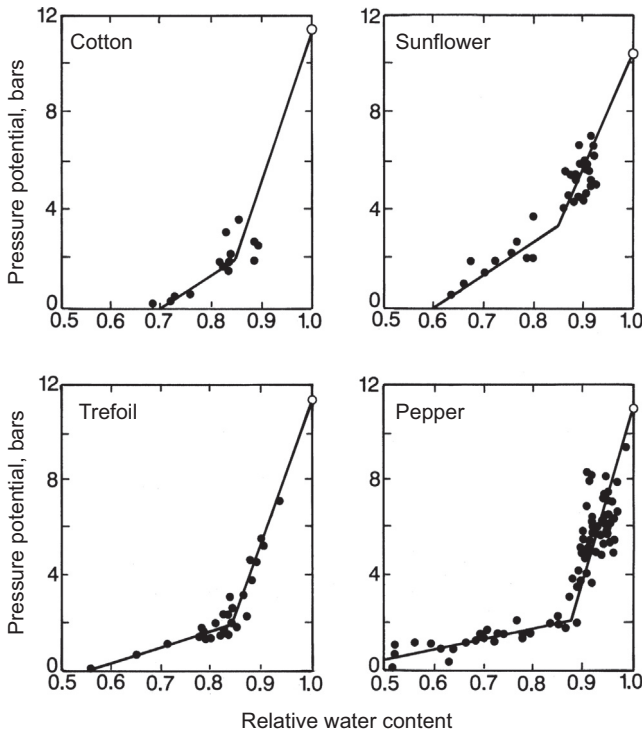


FIGURE 23.6 Pressure potential of the plant leaf as a function of the relative water content. The pressure potential at a relative water content of unity was taken numerically equal to the osmotic potential at this water content in [Figure 23.3](#). From [Gardner and Ehlig \(1965\)](#), *American Society of Plant Physiologists*. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.

modulus of elasticity for each range. The change in the elasticity occurs at about 2 bars for cotton, trefoil, and pepper, and at about 3.5 bars for sunflower.

Gardner and Ehlig (1965) then looked at the elastic properties of a leaf along different axes (in plane of the leaf and perpendicular to the plane of leaf) (length elasticity or Young's modulus). To investigate this, they determined the areas of the individual leaf disks as a function of relative water content (Figure 23.7). They divided the relative water content (as noted, an indication of volume) by the relative area to obtain the thickness of the leaf disks (Figure 23.8). Note that the data in Figure 23.8 fall on a straight line above a water content of about 0.4, but tend to curve toward the origin at lower water contents. The curvilinear part of the curve is explained by assuming that the water bound in the cell walls does not contribute to the expansion of the leaf. The straight line portion of the curve is displaced upward because of this water. On extrapolating the curves in Figure 23.8 back to zero relative water content, the quantity of water involved can be estimated. This turns out to be 15% for cotton and approximately 10% for sunflower, trefoil, pepper,

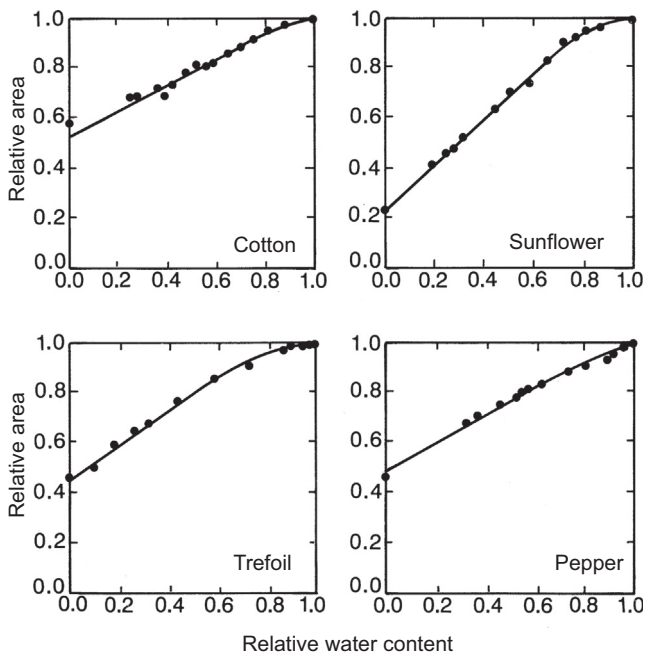


FIGURE 23.7 Relative area of leaf disks as a function of relative water content. From Gardner and Ehlig (1965), *American Society of Plant Physiologists*. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.

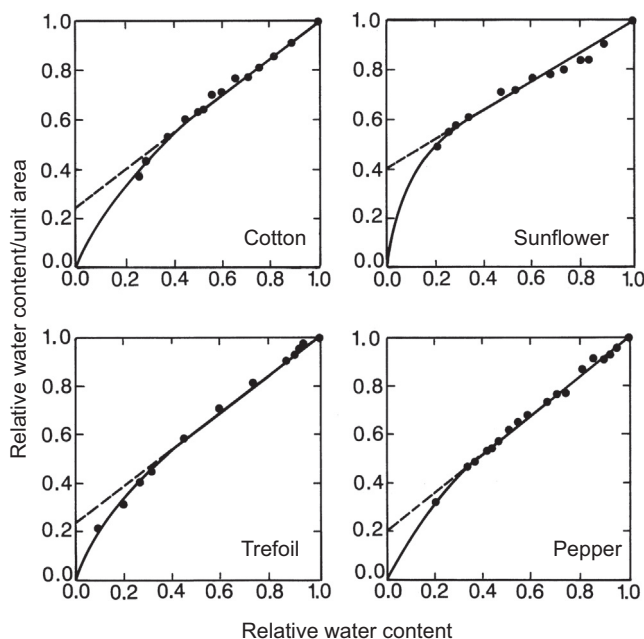


FIGURE 23.8 Relative water content per unit area as a function of the relative water content. This ratio gives a measure of leaf thickness. From [Gardner and Ehlig \(1965\)](#), *American Society of Plant Physiologists*. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.

and pepper, relative to the fully turgid condition. (In [Figure 23.8](#), read from the dashed line on the ordinate horizontally over to the solid line, and then read the corresponding relative water content on the abscissa.)

The relative diameter and the relative thickness are plotted in [Figure 23.9](#) as a function of pressure potential (turgor pressure or turgor potential). Most of the increase in volume with increasing turgor pressure occurs in the leaf thickness with only a small increase occurring in the lateral dimensions of the leaf. All four species studied exhibited nearly the same moduli of elasticity in the high turgor pressure range, with more variation between species in the low-pressure range. Values for the elastic moduli taken from the slopes of the lines in [Figures 23.6 and 23.9](#) are given in [Table 23.1](#). Ordinarily, the elastic modulus is defined in terms of the increase in a dimension relative to that dimension when there is zero stress. However, it is much more difficult to fix precisely the point of zero turgor than the point of maximum turgor. For this reason, the moduli in [Table 23.1](#) were calculated with respect to a relative water content of 1.0.

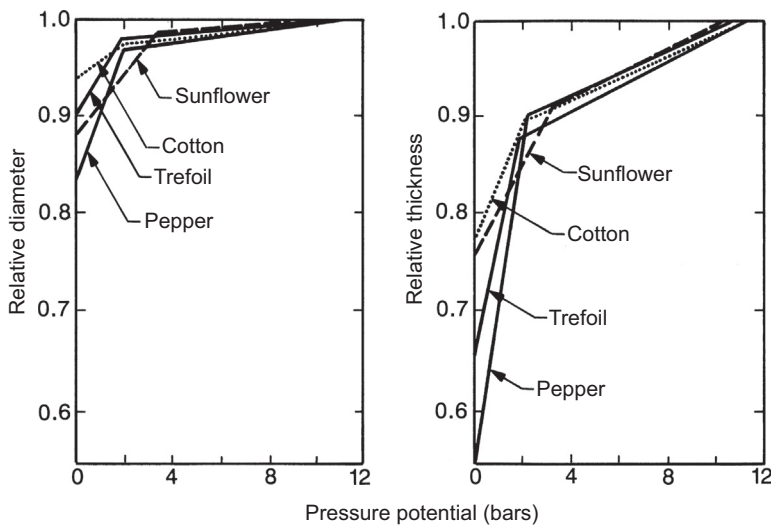


FIGURE 23.9 Relative diameter and relative thickness of leaf disks as a function of the pressure potential. The slopes of these lines are proportional to the moduli of elasticity. From *Gardner and Ehlig (1965)*, American Society of Plant Physiologists. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.

We can compare the values for moduli of elasticity in [Table 23.1](#) to those of nonliving materials ([Table 23.2](#)). (To compare units in [Tables 23.1](#) and [23.2](#), remember that $1\text{ N/m}^2=10\text{ dyn/cm}^2$ because $1\text{ N}=10^5\text{ dyn}$ and $1\text{ m}^2=10^4\text{ cm}^2$. For example, brass has a bulk modulus of $10\times10^{10}\text{ N/m}^2$. This equals $10\times10^{11}\text{ dyn/cm}^2$.) Comparing [Tables 23.1](#) and [23.2](#), we see

TABLE 23.1 Moduli of Elasticity

Species	Turgor Pressure Range (bars)	Bulk Modulus (dyn/cm ²)	In Plane of Leaf (dyn/cm ²)	Perpendicular to Plane of Leaf (dyn/cm ²)
Cotton	>2	6.0×10^7	42.0×10^7	8.1×10^7
	<2	1.5×10^7	5.0×10^7	2.0×10^7
Sunflower	>3.4	4.7×10^7	46.5×10^7	7.9×10^7
	<3.4	1.4×10^7	3.3×10^7	2.3×10^7
Trefoil	>2	6.0×10^7	48.0×10^7	7.7×10^7
	<2	0.63×10^7	2.6×10^7	0.85×10^7
Pepper	>2	7.1×10^7	35.5×10^7	9.9×10^7
	<2	0.44×10^7	1.6×10^7	0.59×10^7

From *Gardner and Ehlig (1965)*, American Society of Plant Physiologists. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.

TABLE 23.2 Typical Elastic Constants

Material	Young's Modulus (N/m ²)	Bulk Modulus (N/m ²)
Aluminum	6.9×10^{10}	... ¹
Brass	9.0×10^{10}	10×10^{10}
Copper	11×10^{10}	14×10^{10}
Nickel	21×10^{10}	...
Steel	20×10^{10}	17×10^{10}
Tungsten	35×10^{10}	...
Glass	5.4×10^{10}	3.6×10^{10}
Ethyl ether	...	0.6×10^9
Ethyl alcohol	...	1.1×10^9
Water	...	2.1×10^9
Mercury	...	28×10^9

¹Not given.

From *Shortley and Williams (1971)*, p. 225. Reprinted by permission of Pearson Education, Inc: Upper Saddle River, New Jersey.

that the bulk modulus of turgid plants is about 10^4 times less than that of nonliving materials. The bulk modulus of wilted plants is about 10^5 times less than that of nonliving materials. The modulus in the plane of a leaf of turgid plants is about 10^3 times less than Young's modulus for nonliving materials. The modulus in the plane of a leaf of a wilted plant is about 10^4 times less than Young's modulus for nonliving materials. A dry cotton fiber has a Young's modulus of 1×10^{11} dyn/cm² (Nobel, 1974; p. 38). (A dry cotton fiber is almost entirely cellulose.) Young's modulus for cotton fibers is about 5% of that for steel. One can see that the moduli of elasticity for plants can be fairly large.

Some interesting conclusions concerning the phenomenon of wilting can be drawn from the data on elasticity (Table 23.1). It has generally been assumed that the permanent wilting point corresponds to zero turgor pressure in the plant leaf. The data (Figure 23.6 and Table 23.1) indicate that visible wilting symptoms occur at a turgor pressure of 2 or 3 bars. Therefore, the visible wilting associated with the permanent wilting point is due to a marked change in the elastic properties of the cell when the turgor pressure drops below a critical value, rather than the complete absence of turgor. This is logical from a physical standpoint. Disregarding the support given to the leaf blade by the veins, the bending of a leaf is similar to the bending of a beam. The extent to which the leaf will flex under its own weight should be inversely proportional to the appropriate

modulus of elasticity and to the cube of the blade thickness (one cubes a leaf dimension to get a volume). When the turgor pressure is above 2 bars, the thickness is relatively constant and little variation in flexure with varying turgor pressure is to be expected. When the turgor pressure is reduced below the critical pressure of about 2 bars, the elastic modulus decreases markedly, allowing the leaf to sag. As the turgor pressure is further reduced, the reduction in leaf thickness tends to permit further bending. The cotton leaf, on one hand, is relatively rigid and is well supported by the veins, so that it exhibits only modest wilting. The pepper leaf, which, on the other hand, is quite elastic and undergoes a considerable change in thickness, shows extreme wilting as the turgor pressure approaches zero (Figure 23.9). The critical turgor pressure at which this change in elasticity is observed corresponds to a water potential of about -11 to -13 bars. This is in good agreement with the traditionally accepted permanent wilting point, which is reasonably well correlated with a soil water potential of -15 bars.

Pressure–volume curves have been used to determine modulus of elasticity of leaves (Melkonian et al., 1982). But we have focused in this chapter on the paper by Gardner and Ehlig (1965), because it relates the physical laws of elasticity (Hooke's law, Young's modulus, bulk modulus) to plant leaves.

23.5 APPENDIX: BIOGRAPHY OF ROBERT HOOKE

Robert Hooke (1635–1703) was an English experimental physicist, who discovered the first law of elasticity for solid bodies, known as Hooke's law. He was born on July 18, 1635, at Freshwater, Isle of Wight (Preece, 1971a).

In 1654, Robert Boyle (1627–1691; English physicist and chemist) settled at Oxford, where he erected a laboratory, kept several operators at work, and engaged, in 1655, Robert Hooke as his chemical assistant. After reading of the air pump of Otto von Guericke (1602–1686; German physicist), Boyle used Hooke's skill to make a less clumsy pump, which was completed in 1659 (Cajori, 1929; p. 78).

On November 12, 1662, Hooke was appointed curator of experiments to the Royal Society, of which he was elected a fellow in 1663, and filled the office during the remainder of his life. In 1665, he was appointed professor of geometry in Gresham College. He was secretary to the Royal Society between 1677 and 1683, publishing in 1681–1682 the papers read before that body under the title of *Philosophical Collections*.

Hooke's optical investigations led him to adopt in 1665 in an imperfect form the undulatory theory of light, which preceded the paper on the wave theory of light presented by Christian Huygens (1629–1695; Dutch

physicist) at the meeting of the French Academy of Sciences in 1678 (Preece, 1971a). (Huygens was induced by Louis XIV to settle in Paris, where he remained from 1666 to 1681 and, like his great contemporaries Newton and Leibniz, Huygens never married.) Hooke was the first to state clearly that the motions of the heavenly bodies must be regarded as a mechanical problem, and he approached in a remarkable manner the discovery of universal gravitation (Preece, 1971a).

Hooke invented the wheel barometer, discussed the application of barometric indications to meteorologic forecasting, and put forward the idea of using the pendulum as a measure of gravity. He is credited with the invention of the anchor escapement for clocks and of the application of spiral springs to the balances of watches (1676) (Preece, 1971a). Hooke died on March 3, 1703, in London. His principal writings are *Micrographia* (1665), *Lectiones Cutlerianae* (1674–1679), and *Posthumous Works*.

23.6 APPENDIX: BIOGRAPHY OF THOMAS YOUNG

Thomas Young (1773–1829), an English physicist and physician, who gave his name to Young's modulus, was born at Milverton, Somersetshire, England, on June 13, 1773 (Preece, 1971b). This great scientist had an extraordinary childhood (Cajori, 1929; p. 148). He could read with fluency at the age of 2. When 4 years old he had read the Bible twice through; at the age of 6 he could repeat the whole of Goldsmith's *Deserted Village*. He devoured books, whether classical, literary, or scientific, in rapid succession. At about the age of 16 years, he abstained from using sugar on account of his opposition to the slave trade. At the age of 19 years, he entered upon a medical education, which was pursued first in London, then in Edinburgh (Scotland), Göttingen (Germany), and finally at Cambridge (England). He began medical practice in London in 1799 (Preece, 1971b). In 1801, he accepted the office of professor of natural philosophy in the Royal Institution, the metropolitan school of science established in the preceding year. He held this position for 2 years. In 1802, he was appointed foreign secretary of the Royal Society and held this office for the remainder of his life. He was elected fellow of the Society in 1794.

Young's earliest studies were on the anatomic and optical properties of the eye; then followed his first epoch of optical discovery, 1801–1804. In 1801, the paper that Young read before the Royal Society dealt with the color of thin plates, in which he supported the undulatory theory of light (Cajori, 1929; p. 149). He made crucial early researches that effectively established the wave theory and was the first to make a thorough application of it to sound and light. He gave the word *energy* its scientific significance (Preece, 1971b).

Young's observations were made with great exactness, but his mode of explaining them was condensed and somewhat obscure (Cajori, 1929; p. 149). His papers, containing the great principle of interference, constituted by far the most important publication on physical optics issued since the time of Newton, yet they made no impression on the scientific public. They were attacked by Lord Brougham in the *Edinburgh Review*. Young's articles were declared to contain "nothing which deserves the name either of experiment or discovery," to be "destitute of every species of merit." "We wish to raise our feeble voice," says Brougham, "against innovations that can have no other effect than to check the progress of science." After stating that the law of interference was "absurd" and "illogical," Brougham said, "We now dismiss, for the present, the feeble lucubrations of this author, in which we have searched without success for some traces of learning, acuteness, and ingenuity, that might compensate his evident deficiency in the powers of solid thinking, calm and patient investigation, and successful development of the laws of nature, by steady and modest observation of her operations." Young issued an able reply, published in the form of a pamphlet, which failed to turn public opinion in favor of this theory (Cajori, 1929; p. 150).

Because his wave theory was laughed at, Young proceeded to other studies. The 12 succeeding years after 1801 were given to medical practice and to the study of philology, especially the decipherment of Egyptian hieroglyphic writing. The Rosetta stone (black basalt, 114 cm long and 71 cm wide) is an ancient Egyptian stone bearing inscriptions in two languages and three scripts: hieroglyphics, demotic (another ancient Egyptian writing), and Greek. It was found in August 1799, by a French man, whose name is given variously as Bouchard or Boussard, during the execution of repairs to the fort of St Julien near the town of Rosetta, or Rashid, on the left bank of a branch of the Nile in the western delta, about 48 km from Alexandria. It passed into British hands with the French surrender of Egypt (1801) and is now in the British Museum, London. The inscription records the commemoration of the accession of Ptolemy V Euphrones to the throne of Egypt in the year 197–196 BC in the ninth year of his reign. The stone gave the key to the translation of Egyptian hieroglyphics hitherto undeciphered (Seton-Williams, 1971).

The decipherment of the hieroglyphic inscription was largely the work of Young and Jean François Champollion (1790–1832; French Egyptologist). Young was the decipherer of the demotic script (Robinson, 2005) and deduced that it was related directly to the hieroglyphics (Kassell, 2006). He discovered that the royal names were written within ovals known as cartouches, and he worked out the names of Ptolemy and Cleopatra. He also discovered in 1814 the way in which the hieroglyphic signs were to be read, by examining the direction in which the birds and animals in this pictorial script faced. The work of these two men established the basis for

the translation of all hieroglyphic texts (Seton-Williams, 1971). One hieroglyph that we recognize today is the ankh, a cross with a loop at the top. It is the symbol for life.

When Augustin Fresnel (1788–1827; French physicist) began to experiment on light and to bring into prominence Young's theory, Young resumed his early studies, and entered into his second great epoch of optical investigation (Cajori, 1929; p. 149). Young died in London on May 10, 1829.

References

- Barrs, H.D., Weatherley, P.E., 1962. A re-examination of the relative turgidity technique for estimating water deficits in leaves. *Aust. J. Biol. Sci.* 15, 413–428.
- Baver, L.D., Gardner, W.H., Gardner, W.R., 1972. *Soil Physics*, fourth ed. Wiley, New York.
- Bowes, B.G., 2000. *A Color Atlas of Plant Structure*. Iowa State University Press, Ames.
- Cajori, F., 1929. *A History of Physics*. Macmillan, New York.
- Ehleringer, J.R., Sage, R.F., Flanagan, L.B., Pearcy, R.W., 1991. Climate change and the evolution of C_4 photosynthesis. *Trends Ecol. Evol.* 6, 95–99.
- Ehlig, C.F., Gardner, W.R., Clark, M., 1968. Effect of soil salinity on water potentials and transpiration in pepper (*Capsicum frutescens*). *Agron. J.* 60, 249–253.
- Esau, K., 1965. *Plant Anatomy*, second ed. Wiley, New York.
- Esau, K., 1977. *Anatomy of Seed Plants*, second ed. Wiley, New York.
- Fahn, A., Cutler, D.F., 1992. Xerophytes: *Encyclopedia of Plant Anatomy* vol. 13. Gebrüder Borntraeger, Berlin. Part 3.
- Gardner, W.R., Ehlig, C.F., 1965. Physical aspects of the internal water relations of plant leaves. *Plant Physiol.* 40, 705–710.
- Hatch, M.D., Slack, C.R., 1966. Photosynthesis by sugar-cane leaves. A new carboxylation reaction and the pathway of sugar formation. *Biochem. J.* 101, 103–111.
- Hatch, M.D., 1992. C_4 photosynthesis: an unlikely process full of surprises. *Plant Cell Physiol.* 33, 333–342.
- Kassell, L., 2006. The last true know-it-all. Book review of *The Last Man Who Knew Everything: Thomas Young, the Anonymous Polymath Who Proved Newton Wrong, Explained How We See, Cured the Sick, and Deciphered the Rosetta Stone, Among Other Feats of Genius*. By Andrew Robinson. Pi Press, New York, 288 pp. *Am. Sci.* 94, 378–379.
- Kirkham, M.B., 2011. *Elevated Carbon Dioxide: Impacts on Soil and Plant Water Relations*. CRC Press, Boca Raton, Florida.
- Laetsch, W.M., 1974. The C_4 syndrome: a structural analysis. *Annu. Rev. Plant Physiol.* 25, 27–52.
- Melkonian, J.J., Wolfe, J., Steponkus, P.L., 1982. Determination of the volumetric modulus of elasticity of wheat leaves by pressure-volume relations and the effect of drought conditioning. *Crop Sci.* 22, 116–123.
- Mellor, R.S., Jensen, R.G., 1986. Photosynthesis: nature's big green machine. *Sci. Food Agr.* 4 (1), 14–19.
- Nobel, P.S., 1974. *Introduction to Biophysical Plant Physiology*. W.H. Freeman and Company, San Francisco.
- Preece, W.E. (Ed.), 1971a. Hooke, Robert. *Encyclopaedia Britannica*, vol. 11, p. 669.
- Preece, W.E. (Ed.), 1971b. Young, Thomas. *Encyclopaedia Britannica*, vol. 23, p. 909.
- Rachidi, F., Kirkham, M.B., Stone, L.R., Kanemasu, E.T., 1993. Soil water depletion by sunflower and sorghum under rainfed conditions. *Agric. Water Manage.* 24, 49–62.
- Robinson, A., 2005. A polymath's dilemma. *Nature* 438, 291.

- Schaum, D., 1961. *Theory and Problems of College Physics*, sixth ed. Schaum, New York.
- Seton-Williams, M.V., 1971. Rosetta Stone. In: *Encyclopaedia Britannica*, vol. 19, 629.
- Shortley, G., Williams, D., 1971. *Elements of Physics*, fifth ed. Prentice-Hall, Englewood Cliffs, New Jersey.
- Slavík, B., 1963. Relationship between the osmotic potential of cell sap and the water saturation deficit during the wilting of leaf tissue. *Biol. Plant* 5, 258–264.
- Torres, A.M., Costello, W.L., 1963. *A Laboratory Manual for General Botany*. Wm. C. Brown, Dubuque, Iowa.
- Woolhouse, H.W., 1978. Light-gathering and carbon assimilation processes in photosynthesis: their adaptive modifications and significance for agriculture. *Endeavour* (New Series) 2 (1), 35–46.