Historical Review

INTRODUCTION

This chapter presents a brief historical review of progress in the field of plant water relations because the authors feel that it is impossible to fully understand the present without some knowledge of the past. As the Danish philosopher Kierkegaarde wrote, "Life can only be understood backward, but it can only be lived forward," and this also is true of science. The present generation needs to be reminded that some generally accepted concepts have their origin in ideas of 17th or 18th century writers and although others were suggested many decades ago, they were neglected until recently.

As might be expected, the importance of water to plant growth was recognized by prehistoric farmers because irrigation systems already existed in Egypt, Babylonia (modern Iraq), and China at the beginning of recorded history, and the first European explorers found extensive irrigation systems in both North and South America. However, irrigation was not used extensively in agriculture in the United States until after the middle of the 19th century and little research on plant water relations occurred until the 20th century.

Early Research

Although plant water relations appear to have been the first area of plant physiology to be studied, progress was slow from Aristotle who died in 322 B.C. to the middle of the 19th century. According to Aristotle, plants absorbed their food ready for use from the soil, and plant nutrition was controlled by a soul or vital principle that allowed plants to absorb only those substances useful in

growth. This idea only began to be questioned in the 17th century by Jung, van Helmont, Mariotte, and others, and it persisted into the 19th century. The early contributions to an understanding of plant water relations were discussed by Sachs (1875, Eng. trans. 1890) and Green (1914). Many early contributions are overlooked. For example, Leonardo da Vinci (1452–1519) observed that the thickness of a tree trunk equals the combined thickness of the branches above it (Zimmermann, 1983, p. 66) and this is supported by later observations (see Chapter 7).

Perhaps the earliest attempt to explain absorption of water by plants was made by the Italian physician and herbalist Andrea Cesalpino in his "De Plantis" published in 1583. After considering and rejecting magnetism and suction, he concluded that roots absorb liquid in the same manner as a piece of linen or a sponge. This must have been one of the earliest attempts to explain a plant process in terms of a physical process. Another physician, J. B. van Helmont (1577–1644), attacked the Aristotelian doctrine of plant nutrition by growing a willow tree for 5 years in a covered pot to which nothing was added but water. As the willow increased in weight by 164 lb. and the soil weight decreased only 2 oz. he concluded that plants use water as food, but he did not try to explain how the water was absorbed or assimilated. An understanding of plant mineral nutrition did not develop until the 19th and early 20th century.

Harvey's publication in 1628 on the circulation of blood in animals increased interest in the possible circulation of sap in plants, and in about 1670 the Royal Society of London sponsored experiments by Ray and Willoughby to learn if sap circulates in plants as it does in animals. Their results were inconclusive, but they did demonstrate that water could move either way in stems. Probably the most important contributions of the 17th century were the anatomical observations of Nehemiah Grew (The Anatomy of Plants, 1682) and Marcello Malpighi (Anatome Plantarum, 1675). Both were interested in physiological processes, and Grew in particular speculated about water absorption and the ascent of sap. Both seemed to think that the sap underwent some change in the leaves that increased is nutritive value, after which it moved to fruits or down to roots, and Malpighi is said to have observed stomata. Although tempting, it is dangerous to reinterpret those old writings in terms of modern plant physiology because of the difficulty in understanding exactly what the writers meant.

The Work of Stephen Hales

The first truly quantitative experiments on plant water relations apparently were those of Stephen Hales, published in his "Vegetable Staticks" in 1727. Hales was a clergyman and humanitarian as well as a physiologist and is known to animal physiologists for his pioneering measurements of blood pressure, published in "Haemostaticks" in 1733. He placed great emphasis on the impor-

tance of plant sap, probably influenced by his work on blood pressure in animals, and made numerous observations on the absorption and translocation of water. Hales wrote, "the most likely way therefore, to get any insight into those parts of the creation, which come within our observation, must in all reason be to number, weigh and measure." This he did to an extent never previously attempted on plants.

Hales measured transpiration of plants of a number of species and calculated root and leaf surfaces from measurements of representative samples, an early use of a sampling technique. He observed that the transpiration rate varied with the species, temperature, time of day, and brightness of the sun, and that although sap exuded from cut grape stems and some trees with considerable force in the spring, exudation ceased later in the season after leaves expanded and water was lost by transpiration, or perspiration as it was then termed. He also observed that water was absorbed through cut stems of transpiring plants. Apparently Hales understood that there is a relationship between absorption and transpiration and regarded absorption as a physical process. There even is some indication that he regarded roots as differentially permeable. His experiments led him to discard the view that sap circulates in plants much as in animals. He seems to have regarded the chief function of leaves as the attraction of sap to the growing regions, although he suggested that light striking leaves might contribute in some way to the nutrition of plants. His observations were published in "Vegetable Staticks" in 1727.

THE CENTURY AFTER HALES

Nearly a century passed before contributions as important as those of Hales were made to the understanding of plant water relations. Early in the 19th century de Saussure (1804) found that the absorption of minerals was not proportional to the absorption of water and that different solutes were not absorbed in the same proportions in which they occurred in the soil, suggesting that roots differ in permeability to various solutes. An example of the unsatisfactory state of physiological knowledge was the wide acceptance of the spongiole theory of A. P. de Candolle (1832). He thought root caps were contractile-absorbing organs and this view was widely accepted for several decades, although an examination of the root tips should have indicated its improbability. Rational explorations of many physical phenomena based on physical and chemical principles were hindered in the early part of the 19th century by the belief that plant and animal processes were controlled by a mysterious "vital force," an idea that apparently originated with Aristotle (Sachs, 1875, pp. 504–509). Perhaps the most important contribution to plant water relations in the first half of the 19th century was development of an osmotic theory by Dutrochet (1837). This was used to explain a variety of phenomena, including the escape of spores from

sporangia and the uptake of water by plants exhibiting root pressure. He also attributed the general condition that we term "turgor" to osmosis. Unfortunately, Dutrochet did not understand the role of differentially permeable membranes in osmosis, but this was developed later in the century by Traube (1867), De Vries (1877), and Pfeffer (1877). The concept of osmosis was philosophically important because important processes previously poorly explained as manifestations of a "vital principle" could now be explained in terms of sound physical processes.

Toward the end of the 18th and the first half of the 19th century advances in chemistry facilitated research on photosynthesis and the mineral nutrition of plants. Identification of oxygen and carbon dioxide and development of methods for measuring gases led to an understanding of gas exchange in photosynthesis by de Saussure and others. The research of Liebig (1841) and later investigators resulted in abandonment of the Aristotelian theory of plant nutrition and development of an understanding of nutrition that forms the basis for modern agricultural practices. However, that lies outside the scope of this book.

THE SECOND HALF OF THE 19th CENTURY

Progress was more rapid after the middle of the 19th century because of advances in chemistry and because more and better trained investigators were involved. Fick (1855) made the first mathematical treatment of diffusion, resulting in Fick's law which still is in use (see Nobel, 1991, pp. 10–12). Graham (1862) differentiated between colloidal and noncolloidal material (crystalloids) and Traube (1867) demonstrated that cell membranes are colloidal. Traube (1867) described how to form artificial membranes that could completely distinguish between small solutes and water, and he proposed a sieve theory of differential permeability and improved on Dutrochet's theory of osmosis. Pfeffer (1877) was the first to accurately measure osmotic pressure, using the membranes of Traube (1867). He recognized that osmotic pressure is determined by the solute concentration in an osmometer (Pfeffer, 1877) but considered cells to have a variable osmotic pressure, sometimes called the turgor pressure (Pfeffer, 1900). He correctly considered the pressure inside cells to arise from the resistance of the cell walls to stretching, which he called turgor. Gibbs (1875–1876) already recognized that, at equilibrium, osmotic pressure balanced the difference in osmotic potential across a membrane, and Pfeffer (1900) occasionally used the potential concept. The idea that protoplasmic membranes can bring about active uptake of solutes against a concentration gradient seems to have originated later with Reid (1890). De Vries (1877) first explained the conditions necessary for development of cell turgor and established a relationship between molecular weight and osmotic pressure that was used by the Swedish chemist Arrhenius to support his ionization theory, which with modifications is in use today.

Modern plant physiology is often said to have begun with the work of Sachs (1882a,b) and his contemporaries in the middle of the 19th century, and this is particularly true of water relations. Sachs (1882a,b) made important investigations of the effects of soil moisture, soil aeration, and soil temperature on water absorption and root growth, and showed that water absorption of warm season plants such as cucurbits is reduced more by cooling the soil than absorption by cool season plants. He also determined that clay soil contains more available water than sandy soil. Sachs demonstrated that water absorption occurs chiefly in the root hair zone instead of through the root tips or spongioles, as proposed by de Candolle. He also believed that transpiration and water absorption are closely related, a view fully developed late in the 19th century by Askenasy (1895) and Dixon and Joly (1895). Sachs mistakenly thought that sap rises in the walls of xylem elements rather than in the lumina because the lumina are often blocked by gas bubbles, but this error was soon corrected by Elfving (1882), Errera (1886), Vesque (1884), and Strasburger (1891). This is discussed further in Chapter 7 in connection with cavitation.

EARLY PLANT PHYSIOLOGY IN THE UNITED STATES

The study of plant physiology in the American colonies and in the early days of the United States lagged far behind England and Europe, partly because the abundance of new plants collected as new regions of the country were explored emphasized plant taxonomy. Among the botanists of prerevolutionary days were Cadwallader Colden of New York who introduced the Linnaean system of classification and John Bartram of Philadelphia whose garden still exists. The latter collected from New York to Florida and sent many specimens to European botanists, including Linnaeus who regarded him as the leading botanist in North America. European visitors such as the Englishman Nuttall, and the Frenchman Michaux who collected in the Southeast, added to the expanding knowledge of American plants. This phase of American botany culminated in the career of Asa Gray who by the middle of the 19th century was recognized in Europe as the dean of American botanists.

Perhaps the earliest research on plant water relations in America was done by Samuel Williams, a native of Vermont, who described it in his book, "The Natural and Civil History of Vermont," published in 1794, and in an enlarged edition in 1809. He wrote that in 1789 he measured the water loss from a detached maple twig, counted the leaves on a maple tree and the number of trees per acre, and estimated the water loss for 12 hr at 3875 gallons per acre, quite reasonable for the methods available. Miller's data (1938, p. 412) indicate an average water loss from an acre of Kansan corn of 3240 gallons per day. Williams also discussed the volume of sap obtained by tapping maple trees, determined the age of trees by counting tree rings, and considered the probable im-

portance of trees in purifying the polluted air of cities. This indicates that air pollution is an old problem, especially in cities where every household burned coal. William's approach to plant water relations suggests that he may have been familiar with the work of Hale, published in 1727.

The botanical textbooks of the 19th century were mostly taxonomic manuals with short discussions of structure. However, Gray's widely used "Lessons in Botany and Vegetable Physiology" with a Preface dated 1857, revised in 1868, contains some physiology. For example, in Chapter XXV he states that most water absorption occurs through the newest root surfaces and that expansion of the root surface is necessary to supply water to the expanding leaf surface. In Chapter XXVI he states, "For in a leafy plant or tree the sap is not forced up from below, but is drawn up from above," a remarkably modern-sounding statement for the time. In Chapter XXV he had stated that most of the water escapes through the stomata. It is evident that he was familiar with the views of European physiologists of his time and incorporated them in his book.

As the supply of new plants dwindled, interest shifted from taxonomy to other areas of botany. In the third quarter of the 19th century W. S. Clark (1874, 1875) made important observations on sap flow and root growth. For example, he found that a squash plant growing in a greenhouse bench produced nearly 16 miles of roots (25 km) and his observations on sap flow from wounds in trees are acceptable today. There seems to have been little further notable work on plant water relations in the United States in the 19th century, although it is possible some interesting work is hidden in unpublished reports and has been overlooked.

THE 20th CENTURY

Burton E. Livingston started his productive career in teaching and research early in the 20th century. His first book, "The Role of Diffusion and Osmosis in Plants" (Livingston, 1903), was quite influential and he later developed apparatus to measure environmental factors, including porous porcelain atmometers to measure evaporation, soil point cones to measure the "water supplying power" of the soil, and lithium chloride clips to measure transpiration. The senior author's first research on plant water relations developed from E. N. Transeau's questions concerning a paper by Livingston (1927). In collaboration with Forrest Shreve (1921), Livingston wrote an important book on the role of climatic factors in plant distribution (Livingston and Shreve, 1921). Most important, he inspired and trained many young people to go into physiological and ecological research, as did the ecologist F. E. Clements. Osterhout also did important research on cell permeability during the early part of this century. Shull (1916) measured the force with which water is held by the soil by comparing the amount of water absorbed by *Xanthium* seeds from soil and from solutions

of various osmotic pressures. He contributed to the development of plant physiology by founding the journal *Plant Physiology*.

Considerable progress was made in Europe in the early part of the 20th century, beginning in 1900 with Brown and Escombe's study of movement by diffusion through small pores such as stomata as a purely physical process. Unfortunately, Brown and Escombe's experiments were conducted in quiet air where the boundary layer resistance is as great as stomatal resistance, and their results indicated that large changes in stomatal aperture have little effect on transpiration. This led to a long and unproductive argument concerning the importance of stomatal control of transpiration. However, later experiments by Stålfelt (1932) and Bange (1953), summarized in Slatyer (1967, pp. 260–269), indicate that stomatal closure has a large effect on transpiration in moving air where the boundary layer resistance is low. Stomatal behavior is discussed in Chapter 8. Lundegårdh's "Environment and Plant Development" (1931) emphasized that the environment acts on plants through its effects on their physiological process.

From Osmosis to Water Potential

One of the important developments of the middle of the 20th century in the field of plant water relations was the shift in emphasis from the osmotic pressure to the water potential of plant tissue as an indicator of plant water status. During the early part of the century thousands of measurements were made of osmotic pressure as an indicator of plant water stress (Korstian, 1924, for example). Some of these data were summarized by Harris (1934). However, it began to be realized that water movement in plants cannot be explained in terms of osmotic pressure gradients, but rather in terms of what is now termed water potential (see Chapter 2). Also there was some uncertainty concerning the reliability of measurements of osmotic pressure. Initially, there was confusion concerning the best terminology and nearly as many terms were used as there were investigators. These included Saugkraft or suction force (Ursprung and Blum, 1916), water-absorbing power (Thoday, 1918), Hydratur (Walter, 1931, 1965), net osmotic pressure (Shull, 1930), diffusion pressure deficit (Meyer, 1938, 1945), and finally water potential (Owen, 1952; Slatyer and Taylor, 1960; Tang and Wang, 1941).

Acceptance of the water potential concept was slow because of the confusion regarding terminology, the lack of convenient methods for measuring it, and the inadequate training of plant physiologists in physical chemistry. As a result, plant water status seldom was measured during the second quarter of the 20th century. Development of thermocouple psychrometers (Monteith and Owen, 1958; Richards and Ogata, 1958; Spanner, 1951) and pressure equilibration by Scholander and his colleagues (1964, 1965) made measurement of water potential relatively easy, and they are the measurements used most often today to

characterize plant water status. Thus although osmotic pressure measurements dominated the first half of the 20th century, the second half was dominated by measurements of water potential. However, interest in osmotic pressure was revived by concern with osmotic adjustment in water-stressed plants (Morgan, 1984; Turner and Jones in Turner and Kramer, 1980). Water potential is now under attack because it is not always well correlated with physiological processes (Sinclair and Ludlow, 1985), but it is defended by Kramer (1988) and Boyer (1989). This is discussed in Chapter 2.

The Permanent Wilting Percentage

In 1911 Briggs and Shantz published their concept of the permanent wilting percentage, which was refined by Richards and Wadleigh (1952), Veihmeyer and Hendrickson (1928, 1950), and others and became widely used. Slatyer (1957) pointed out that instead of being a soil constant, the permanent wilting percentage really depends on the water potential at which leaves lose their turgor, which depends on their osmotic properties and the meteorological conditions affecting transpiration, and on soil conditions that affect water absorption. Although there is no sharply defined lower limit for availability of water to plants (Gardner and Nieman, 1964; Hagan *et al.*, 1959), the permanent wilting percentage is a useful concept. It is discussed in more detail in Chapter 4.

The Absorption of Water

Although water absorption has been discussed since the time of Aristotle, textbook discussions in the first half of the 20th century were disappointingly vague concerning the mechanism. For example, Miller (1938) stated that imbibition, osmosis, and passive absorption apparently were involved, but he doubted if these forces provided an adequate explanation. This is surprising because Renner (1912, 1915) had already distinguished between the "active" absorption mechanism operating in slowly transpiring plants and the "passive" mechanism operating in rapidly transpiring plants. Renner's views were reinvestigated and expanded by Kramer (1932, 1937, 1939, 1940b) and it is now generally accepted that although roots of slowly transpiring plants act as osmometers, water is "pulled" in passively through the roots of rapidly transpiring plants. It also became possible to distinguish between effects of environmental stresses such as low temperature and deficient aeration on root resistance (conductance or permeability) to water flow and on the driving force causing water movement. Water absorption is discussed in more detail in Chapter 6.

SOME GENERAL CONCEPTS

By the middle of the 20th century much valuable information was available, but it was poorly organized. However, several general concepts became avail-

able which have been useful in organizing information and research on plant water relations.

Plant Water Balance

One useful idea is the concept of plant water balance, proposed by Montfort (1922) and Maximov (1929). This treats plant water status as dependent on the relative rates of water absorption and water loss in transpiration. Although these two processes are coupled by the cohesive columns of xylem sap, they do not always operate synchronously because of the capacitance factor provided by water stored in the parenchyma cells of leaves, stems, and roots. Thus water absorption often lags behind transpiration in the morning (Fig. 6.1), resulting in loss of turgor and temporary wilting by midday, even in plants growing in moist soil. This led to the view that plant water status cannot be predicted reliably from measurements of soil moisture, but must be measured directly on the plant (Kramer, 1963).

Soil–Plant–Atmosphere Continuum and Ohm's Law Analogy

Another useful, unifying concept is that of the soil–plant–atmosphere continuum (SPAC) which seems to have been proposed by Huber (1924), developed by Gradmann (1928) and Honert (1948), and brought into general use by Slatyer and Taylor (1960), Rawlins (1963), and others. This concept emphasizes the interrelationships of soil, plant, and atmospheric factors in determining plant water status. As the equation for water flow through the SPAC resembles that for flow of electricity in a conducting system it is often termed the Ohm's Law analogy. Cowan (1965) used this concept to produce a model showing resistances and capacitances in the SPAC. Although very convenient for teaching and analyzing the way in which various factors affect water flow through the soil–plant–atmosphere continuum, it is an oversimplification because it assumes steady-state flow and constant resistance, conditions that seldom exist. Some of the difficulties with the water potential terminology were discussed by Passioura (1982), and Fiscus and Kaufmann (in Stewart and Nielson, 1990, p. 228) argue that the Ohm's Law analogy has no advantage over a fluid transport law and should be abandoned. However, we think it is too useful to be abandoned. Johnson et al. (1991) discuss the integration of new concepts into a satisfactory model of water flow.

Kleb's Concept

A third useful concept, shown in Fig. 1.1, indicates how hereditary potentialities and environmental factors such as water stress act through physiological processes to determine the quantity and quality of plant growth. This concept is based on ideas of a German physiologist, Klebs (1910, 1913). Kleb's concept

HEREDITARY POTENTIALS

Depth and extent of root systems

Size, shape and total area of leaves, and ratio of internal to external surface

Number, location, and behavior of stomata

ENVIRONMENTAL FACTORS

SOIL. Texture, structure, depth, chemical composition and pH, aeration, temperature, waterholding capacity, and water conductivity
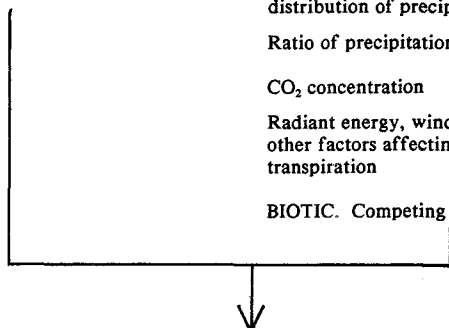
ATMOSPHERIC. Amount and seasonal distribution of precipitation

Ratio of precipitation to evaporation

CO_2 concentration

Radiant energy, wind, vapor pressure, and other factors affecting evaporation and transpiration

BIOTIC. Competing plants, diseases, insects

PLANT PROCESSES AND CONDITIONS

Water absorption

Ascent of sap

Transpiration

Internal water balance as reflected in water potential, turgidity, stomatal opening, and cell enlargement

Effects on kinds and amounts of growth regulators, photosynthesis, respiration, carbohydrate and nitrogen metabolism, and other metabolic processes

QUANTITY AND QUALITY OF GROWTH

Size of cells, organs, and plants

Dry weight, succulence, kinds and amounts of various compounds produced and accumulated

Root-shoot ratio

Vegetative versus reproductive growth

Figure 1.1 A diagram showing how the quantity and quality of plant growth are controlled by hereditary potentialities and environmental factors operating through the physiological processes and conditions of plants, with special emphasis on effects of water.

emphasizes the fact that environmental factors such as water stress operate through physiological processes to affect the quantity and quality of plant growth, within the limits permitted by heredity. It is useful in organizing ideas and emphasizes the fact that environmental factors such as drought or irriga-

tion, cultural practices, and plant breeding affect crop yield by modifying the efficiency of essential physiological processes.

THE SITUATION TODAY

There has been great progress in our understanding of plant water relations during the 20th century and in the development of new instrumentation that facilitates research (Hashimoto *et al.*, 1990). As a result of the increase in research and publication, one of the most troublesome problems today is that of keeping up with the current literature. While computerized bibliographies are helpful, they cannot distinguish between important and trivial papers. Furthermore, what seems trivial to one reader may be important to another or when read in a different context.

Changing Viewpoints

The accumulation of new information often requires the revision of existing explanations. Many so-called scientific explanations are "true," only in the sense that they represent the most logical conclusions that can be drawn from our present information, and the acquisition of additional information may require their revision. For example, it has been assumed for many years that shoot and leaf turgor control cell expansion, stomatal conductance, and photosynthesis. However, research by Shackel *et al.* (1987), Zhu and Boyer (1992), and others indicates that cell enlargement depends on cell wall metabolism as well as turgor. Several experiments discussed by Schulze (1986a), Turner (1986, pp. 13–15), Davies and Zhang (1991), and Davies *et al.* (1994) suggest that stomatal conductance and photosynthesis are better correlated with soil and root water status than with leaf water status. Kramer (1988) expressed reservations concerning the broad application of the conclusions from split-root pot experiments to plants in nature. In any event there is increasing interest in the importance of biochemical signals such as cytokinin and abscisic acid (ABA) transmitted from roots to shoots that affect physiological processes in the shoots. This is discussed in more detail in Chapters 6, 9, and 11.

Also, after several decades of emphasis on the plant water potential as a good indicator of plant water status, some investigators are claiming that physiological processes are better related to relative water content than to water potential (Sinclair and Ludlow, 1985). As pointed out earlier, there has been considerable interest in osmotic adjustment as a factor in drought tolerance (Morgan, 1984) but this idea also is now being questioned (Munns, 1988). Considerable uncertainty concerning the relative importance of stomatal and nonstomatal inhibition of photosynthesis in water-stressed plants also exists (Farquhar and Sharkey, 1982; also see Chapter 10). Even the cohesion theory of the ascent of sap is under attack by some investigators (see Balling and Zimmermann, 1990; Zimmerman *et al.*, 1993). This is discussed in Chapter 7.

Bound water was once regarded as an important factor in drought and cold tolerance (Kramer, 1955), but it has been neglected in recent years. However, development of new methods for measuring it, such as the water sorption isotherm (Vertucci and Leopold, 1987a,b), nuclear magnetic resonance (NMR) spectroscopy (Burke et al., 1974; Kramer et al. in Hashimoto et al., 1990; Roberts, 1984), and NMR imaging (G. A. Johnson et al., 1987; Veres et al., 1991), are likely to result in a renewed study of bound water as a factor in the tolerance of dehydration and freezing.

Increasing Emphasis at the Molecular Level

There is likely to be more research on the effects of water deficits on physiological processes at the molecular level. For example, water deficits seem to increase some enzymatically mediated processes but to decrease others (Hsiao and Bradford in Taylor et al., 1983). Chapter 9 discusses enzyme responses and suggests a hypothesis to account for them (see Regulator Hypothesis of Enzyme Control). Root/shoot communication is being increasingly studied at the molecular level, and Chapter 9 discusses an example for the enzyme nitrate reductase where control of the shoot enzyme is determined by the delivery of nitrate from the roots. Ho and Mishkind (1991) reported that a water deficit caused appearance of some new mRNAs and disappearance of others in water-deficient tomato leaves, and cited other research showing the appearance of new proteins in these plants. Molecular work also opens up the prospect of increasing the tolerance to unfavorable conditions by altering the genetic potential of plants. Tarczynski et al. (1993) increased the salt tolerance of tobacco plants by introducing a bacterial gene that increased their capacity to synthesize mannitol, and Potrykus (1991) surveyed methods used to transfer genes and some results obtained. The direction of future research is indicated by some papers in Close and Bray (1993). These include discussion of the role of special proteins such as dehydrin and osmotin and accumulation of proline, glycine betaine, and quaternary ammonium and tertiary sulfonium compounds in water-deficient and salinized plants that are also discussed in Chapters 3 and 12. Other examples of current trends are the study by Thomas and Bohnert (1993) of the induction by salt stress of plant growth regulators, the effects of phosphorus deficiency on root metabolism (Johnson et al., 1994), and the study of the varying role of hormones on root development of water-deficient Arabidopsis (Vartanian et al., 1994). Chrispeels and Maurel (1994) found that special proteins form water channels in membranes (see Chapter 3). These studies show that molecular genetics is being increasingly used in physiological research, and the May, 1994 issue of Plant, Cell and Environment contains 16 papers on the use of mutants and transgenic plants in physiological studies.

The current interest in research at the molecular level is very important, but it should not obscure the fact that there is still need for research on water rela-

tions at the whole plant level. The success of crop plants depends primarily on the avoidance of stress, which depends on the success of leaves in controlling water loss and the effectiveness of roots in absorbing water in competition with other plants. It is true that tolerance of dehydration depends on characteristics at the cellular and molecular level, such as osmotic adjustment, the water-binding capacity of tissues, and the manner in which water stress affects enzyme-mediated processes, and it is likely that research at that level will make important contributions in this area. However, the successful growth of economic plants depends more on the avoidance than on the tolerance of severe water stress, and severely water-stressed crops seldom are profitable. Avoidance of severe water stress requires coordination at the whole plant level between control of water loss from transpiring shoots and water absorption through root systems. Thus from a practical standpoint, research at the whole plant level remains very important. Furthermore, a good understanding of whole plant structure and physiology is essential for the effective application of molecular biology to the solution of problems in the field and forest. This is discussed in Chapter 12.

SUMMARY

For nearly 2000 years after the observation of the early Greek philosophers, Aristotle and Theophrastus, there were no important contributions to plant physiology. In the 17th century Grew and Malpighi published on plant anatomy and speculated about plant processes, but the first quantitative studies of plant water relations were not published until 1727, by Hales. Advances in chemistry toward the end of the 18th and early 19th century permitted a better understanding of photosynthesis and mineral nutrition.

Modern plant physiology began to develop after the middle of the 19th century with the work of Sachs, Strasburger, and other German plant scientists. Early plant research in North America was concerned chiefly with the classification of plants brought home by explorers. However, Gray's textbooks, published after the middle of the 19th century, contained some physiology, apparently derived largely from European publications. After the beginning of the 20th century there was a worldwide increase in research on plant water relations, including work on soil moisture, root systems, and measurement of plant water status. In the United States the early research occurred chiefly in agricultural experiment stations, at a few universities, and at the Desert Laboratory at Tucson, Arizona.

Toward the middle of the 20th century emphasis began to shift from osmotic pressure to water potential as an indicator of plant water status. This was facilitated by the introduction of pressure equilibration and thermocouple psychometers to measure water potential. At present there is expanding research at the cellular and molecular level which will increase our understanding of how water

stress injures plants and how to increase tolerance of water stress. Several concepts were developed which are useful in organizing our information concerning plant water relations. One is the concept of the plant water balance as controlled by the relative rates of water absorption and loss, another is the treatment of water as constituting a continuum in the soil–plant–atmosphere system. Another more general concept states that heredity and environment act through physiological processes to determine the quantity and quality of growth. These concepts have assisted in organizing information more effectively and in planning research.

In conclusion, we are in a period of change when some long established concepts are being questioned and new explanations are being proposed. Furthermore, research emphasis is shifting from the whole plant to the cellular and molecular level. The authors have attempted to evaluate some conflicting explanations and to support those that seem most logical. However, as more information becomes available it may become necessary to modify or even abandon some of our present beliefs and explanations.

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