C H A P T E R

19

Pressure Chambers

The pressure chamber described by Scholander and colleagues (1964, 1965) is the most popular method used to measure water potential of plants. (For a biography of Scholander, see the Appendix, Section 19.5.) The method consists of increasing the pressure around a leafy shoot until sap from the xylem appears at the cut end of the shoot, which extends outside of the chamber and is exposed to atmospheric pressure (Figures 19.1 and 19.2). The pressure necessary to retain this condition represents the negative pressure existing in the intact stem. It is felt that the amount of pressure necessary to force water out of the leaf cells into the xylem is a function of the water potential of the leaf cells (Boyer, 1967).

19.1 COMPARISON OF MEASUREMENTS MADE WITH THE PRESSURE CHAMBER AND THE THERMOCOUPLE PSYCHROMETER

For accurate measurements, one should compare measurements made with a thermocouple psychrometer with those made with a pressure

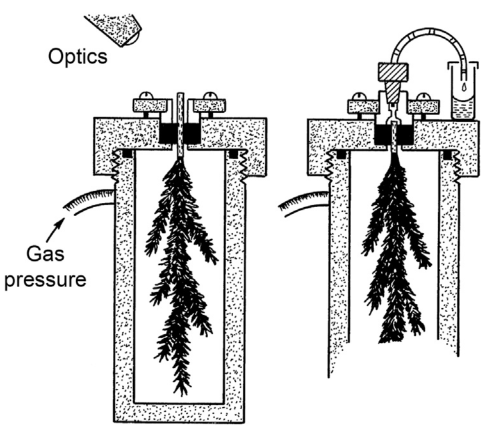

FIGURE 19.1 Pressure chamber for measurement of sap pressure in the xylem of a twig. Left: direct observation; right: stepwise sap extrusion and pressure measurement to obtain a pressure–volume curve. *Reprinted with permission from Scholander et al. (1965), American Association for the Advancement of Science.*

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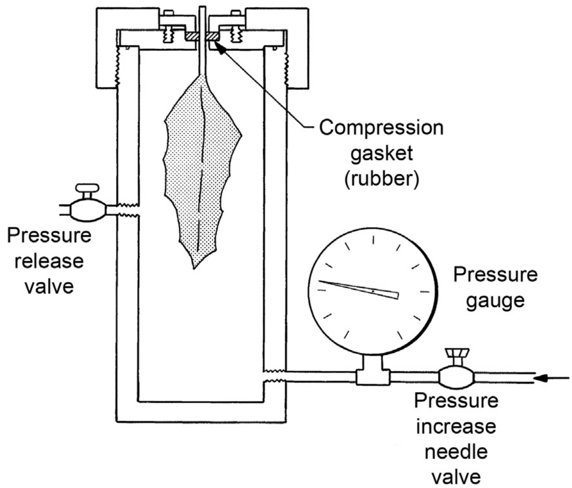

FIGURE 19.2 Diagrammatic cross-section through a pressure chamber for measurement of leaf water potential by pressure equilibration. *From Kramer (1983). Reprinted by permission of Academic Press.*

chamber before assuming that the pressure chamber is giving valid measurements of water potential. Because the thermocouple-psychrometer method is based on sound physics using the Kelvin equation (Rawlins, 1972), measurements made with thermocouple psychrometers are the standard ones. But relatively few comparisons exist in the literature. Most people take for granted that the pressure chamber is giving an accurate measurement of water potential and most people use the pressure chamber when measuring plant water potential. It has the advantages of relative simplicity and provision of pressure—volume curves to estimate osmotic potential and turgor potential (see Chapter 17).

Boyer (1967) was one of the first to compare measurements made with thermocouple psychrometers with those made with a pressure chamber. (For a biography of Boyer, see the Appendix, Section 19.6.) He estimated leaf water potentials from the sum of the balancing pressure measured with a pressure chamber and the osmotic potential of the xylem sap in leafy shoots or leaves of yew (*Taxus cuspidata* Sieb. & Zucc.), rhododendron (*Rhododendron roseum* Rehd.), and sunflower (*Helianthus annuus* L.). Measurements made with the pressure chamber were within ±2 bar of the psychrometric measurements with sunflower and yew (Figures 19.3 and 19.4). In rhododendron, water potentials measured with the pressure chamber plus xylem sap were 2.5 bar less negative to 4 bar more negative than the psychrometric measurements (Figure 19.5). As we shall see when we discuss the ascent of sap in plants (Chapter 20), xylem sap is very dilute. Boyer (1967) found xylem sap in yew, rhododendron, and

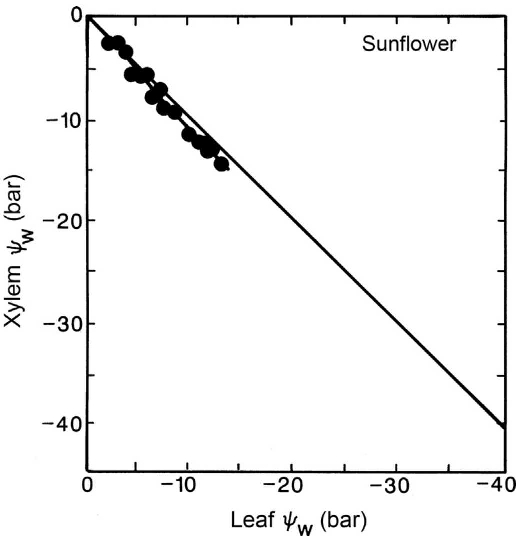

FIGURE 19.3 Xylem and leaf water potentials in sunflower. The equipotential values are represented by the diagonal line. Each point represents a single determination. *From Boyer (1967), American Society of Plant Physiologists. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.*

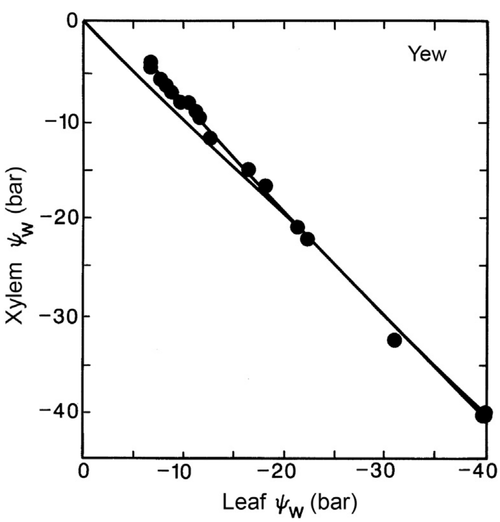

FIGURE 19.4 Xylem and leaf water potentials in yew. The equipotential values are represented by the diagonal line. Each point represents a single determination. *From Boyer (1967), American Society of Plant Physiologists. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.*

sunflower to have a solute potential of about −0.5 bar (Figure 19.6). Only when plants got very stressed (e.g., when the rhododendron leaves were at −30 bar) was the xylem sap about −2.0 bar. So the solute potential of the sap was usually within the error of comparison (±2 bar). When making measurements with pressure chambers, the osmotic potential of the xylem sap is ignored, and it is assumed that the balancing pressure is the water potential of the leaves.

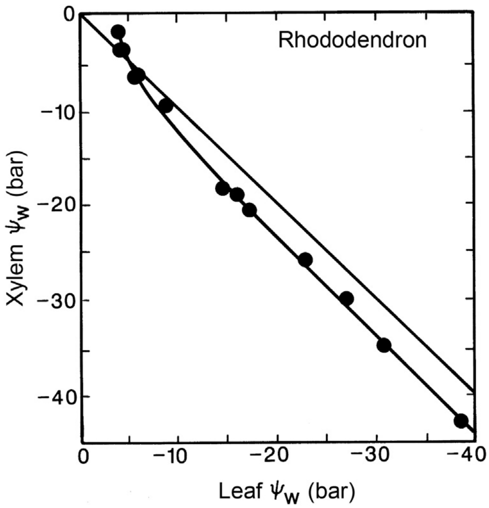

FIGURE 19.5 Xylem and leaf water potentials in rhododendron. The equipotential values are represented by the diagonal line. Each point represents a single determination. *From Boyer (1967), American Society of Plant Physiologists. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.*

Gandar and Tanner (1975) compared potato (*Solanum tuberosum* L.) leaf and tuber water potentials measured with both a pressure chamber and thermocouple psychrometers. They used soil psychrometers to measure the tuber water potential. They bored holes in the tuber and put the soil psychrometer in the hole. For leaves drier than −3 bar, the pressure chamber gave estimates of water potential that were 0−3 bar drier than potentials measured using thermocouple psychrometers. Pressure chamber readings ranged ±2.5 bar from the psychrometric value for leaves wetter than −3 bar. The psychrometric measurement usually was drier than that obtained using the pressure chamber when leaves were sampled in the evening. With tubers, water potential measurements using the in situ soil psychrometers and the pressure chamber agreed to within 1 bar, except in tubers drier than −7 bar, in which there were discrepancies of ±2.5 bar. However, if the interval between psychrometer insertion and water potential measurement was longer than 24 h, serious errors arose in the psychrometer measurements, apparently from suberization of tissues surrounding the psychrometers that prevented vapor equilibrium.

19.2 ADVANTAGES AND DISADVANTAGES OF THE PRESSURE CHAMBER

The Scholander pressure chamber is commercially available (Figures 19.7−19.9), and it is widely used (Cochard et al., 2001) because of its many advantages. They include simplicity, comparative speed of measurement,

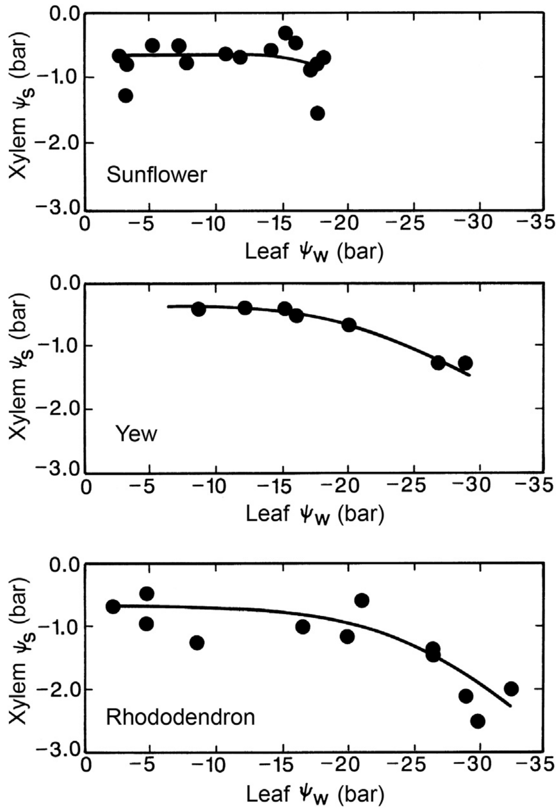

FIGURE 19.6 Xylem osmotic potentials (xylem Ψ_s) measured at various leaf water potentials in sunflower, yew, and rhododendron. Each point represents a single determination. *From Boyer (1967), American Society of Plant Physiologists. Reprinted by permission of the American Society of Plant Biologists, Rockville, Maryland.*

and fair portability (Oosterhuis et al., 1983). Even though thermocouple psychrometers appear to provide more accurate measurements than pressure chambers (Millar, 1982) and are based on sound theory, they are not used widely, because they require patience and experience before meaningful data can be obtained. In addition, precise temperature control is needed.

However, care also is necessary to gather accurate readings with a pressure chamber. Samples must be protected against transpiration following excision. They must be measured immediately. In field experiments, the pressure chamber has to be protected against wind, so the exuded sap does not evaporate before a measurement can be recorded. When conditions are windy, the pressure chamber can be put in the open hatchback of a van. An operator can stand outside the van on the ground

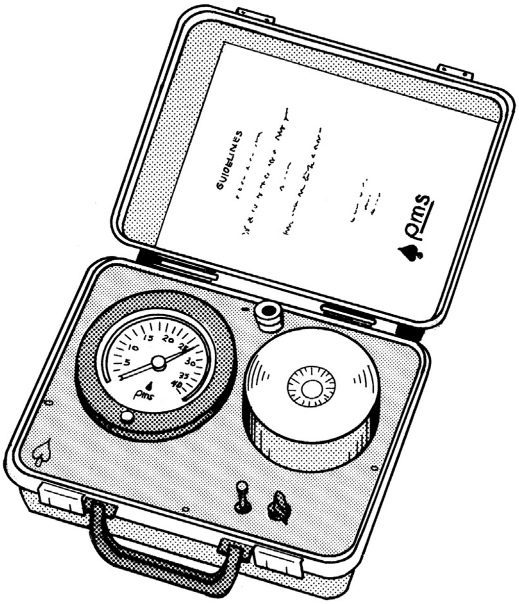

FIGURE 19.7 A commercially available pressure chamber. The pressure chamber is designed for either laboratory or field use. A safety valve on the lug cover ensures that pressure can be applied to the chamber only when the cover is properly and completely secured. The gas tank is an accessory and is not shown. *From a PMS Instrument Company, Corvallis, Oregon, brochure. Reprinted by permission of PMS Instrument Company.*

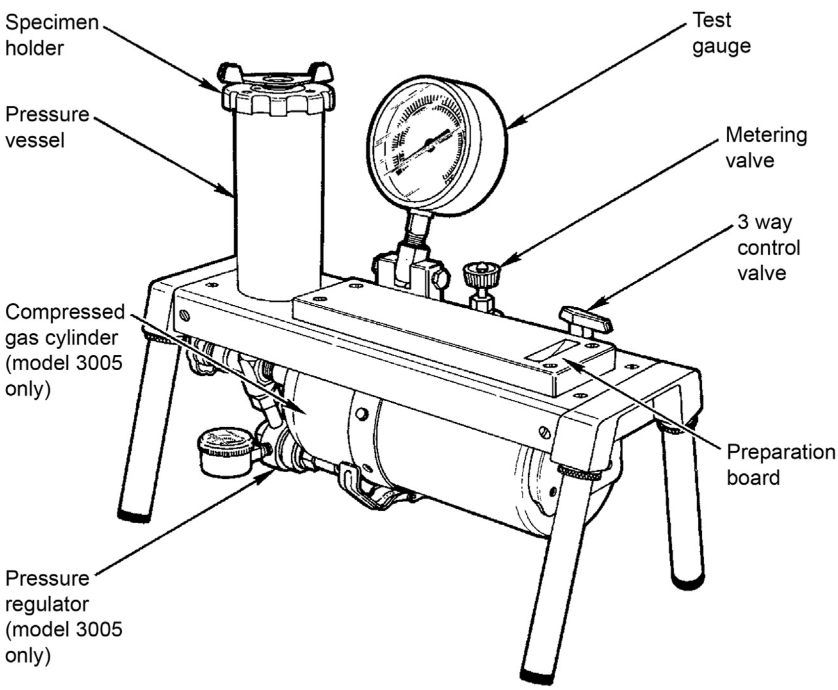

FIGURE 19.8 A commercially available pressure chamber, the Plant Water Status Console. A canister of gas is attached to the bottom of the hardwood base, making the unit self-contained. *Courtesy of Soilmoisture Equipment Corp., Santa Barbara, California.*

FIGURE 19.9 A commercially available, portable pressure chamber made by Soilmoisture Equipment Corp., Santa Barbara, California. *Photograph courtesy of Marsha K. Landis, Graphic Designer, Kansas State University, Manhattan, Kansas.*

and use a magnifying glass to see the endpoint. The plant sample itself is out of the wind. If a large field is being sampled, "runners" carry the sample from the field to the pressure chamber, so a reading can be made within a matter of seconds after the stem has been cut. Sometimes samples are protected against water loss by putting them in a container with wet cheesecloth and then taking them to the pressure chamber. But the wet cheesecloth could provide water to the sample and result in an erroneous measurement.

Low pressurization rates must be used to avoid false endpoints (Tyree et al., 1978; Wenkert et al., 1978; Karlic and Richter, 1979; McCown and Wall, 1979; Turner and Long, 1980; Brown and Tanner, 1981; Leach et al., 1982). Brown and Tanner (1981) suggest that the pressurization rate should be 0.006 MPa/s (0.06 bar/s).

If the proper technique is used, measurements made with pressure chambers can agree with those made with thermocouple hygrometers (Faiz, 1983; Walker et al., 1983). Values for the flow of water through stems, obtained by applying pressure to plants in a pressure chamber, also agree with those obtained by applying vacuums to plants with vacuum pumps (Dryden and van Alfen, 1983).

The Scholander pressure chamber is not well suited to measurements of small plants such as grasses because a petiole must extend through the seal of the pressure chamber. Plants with tender tissues (e.g., new tillers on grasses) are easily damaged by the seal and cannot be used. "Telescoping" of inner leaves of grass tillers at high pressure is another problem. The inner leaves are pushed out of the seal by the high pressures in the chamber. Leaves of a substantial size must be sampled, and, if they exist in an experiment, the sampling results in rapid denudation of leaves. This is a problem in studies with limited plant material.

Large stems, like those of mature sunflower plants, cannot be measured, because commercially available pressure chambers do not have rubber grommets, which make the seal, wide enough to accommodate the large stems. There is an interest in exuding sap from plants such as sunflower in phytoremediation studies to determine if the pollutant has been taken up by the plant. If the stem is too big for the pressure chamber, the sap cannot be exuded.

Pressure chambers are heavy and cumbersome, not only because they require a heavy tank of high-pressure gas, but also because the equipment itself is heavy. The gas supply limits the number of measurements that can be made in the field. The use of high-pressure gas can be dangerous for two reasons: (1) If not noncombustible, it is a fire hazard; (2) Plants can blow out of the chamber and hit a person in the eye. The commercially available pressure chambers (Figures 19.7–19.9) use nitrogen (N_2) gas, which is noncombustible. One must always wear glasses or safety glasses when using a pressure chamber, in case the sample blows out of the chamber and hits the eye.

Even though a measurement with a pressure chamber is faster than with a thermocouple psychrometer, it still takes about 5 min per sample. Pressure chambers and the constant supply of gas are expensive. Relatively unskilled workers can take measurements with a pressure chamber, but some training is required for reliable readings.

19.3 HYDRAULIC PRESS

The hydraulic press operates on the same principle as the pressure chamber, yet overcomes some of the pressure chamber's limitations (Campbell and Brewster, 1975). The press consists of a commercial 1.5 ton (1360 kg) hydraulic automobile jack modified to apply pressure through a thin rubber membrane covered with nylon (a lady's stocking) to a leaf sample, which is observed through a 1.27 cm thick Plexiglas plate (Campbell and Brewster, 1975; Jones and Carabaly, 1980). The instrument applies pressure to a leaf and squeezes the leaf between the membrane and a Plexiglas plate. When the applied pressure equals the water potential, cell walls and intercellular spaces become saturated. The leaf color changes (becomes darker) at this pressure, so that the pressure then can be read on a dial gauge attached to the jack. The hydraulic press can be used not only with leaves but also stems, twigs, needles, and soil.

The hydraulic press used to be available commercially, but it no longer can be bought. However, it represents a type of instrument that is useful in soil–plant–water relations. It has several advantages. A variety of soils and plants can be measured, including tender leaves and tillers. It weighs only 5 kg. It is rugged and never breaks down. Only the nylon stocking needs to be replaced occasionally. No high-pressure gas is required. Measurements are fast (about 20 s per sample), and inexperienced workers also can use it.

The main disadvantage of the hydraulic press appears to be that it does not have a sound theoretical basis (Shayo-Ngowi and Campbell, 1980). It is also difficult to get precise readings. But, because of its advantages, the instrument deserves study by theoreticians and plant physiologists. What, for example, is the effect of pressure on leaf cells? Why can a leaf in the hydraulic press turn completely black under pressure and then immediately spring back to its normal green color and apparent turgidity once the pressure is released?

19.4 PUMP-UP PRESSURE CHAMBER

Around the year 2000, Plant Moisture Stress (PMS) Instrument Company in Corvallis, Oregon, introduced a new type of pressure chamber (Figure 19.10). It is different from the conventional gas chamber in that it does not require a source of compressed gas such as nitrogen, which can be dangerous to use, as noted in Section 19.2. The pressure required to take water-potential readings is created by pumping the instrument as one would a bicycle pump. The relatively small chamber allows the user to achieve about 0.5 bar (7.25 psi) pressure per stroke (Figure 19.11). The instrument is limited to 20 bar and is designed primarily for irrigation scheduling and monitoring, particularly for managing deficit irrigation. A picture of the instrument in use is shown by Goldhamer and Fereres (2001).

19.5 APPENDIX: BIOGRAPHY OF PER SCHOLANDER

Per Fredrik Scholander a physiologist, was born in Örebro, Sweden, on November 29, 1905, and he married in 1951 (American Men of Science, 1961). He got his M.D. degree in Oslo in 1932 and his PhD in botany in 1934. He was an instructor of anatomy in Oslo between 1932 and 1934 and was a research fellow in comparative physiology between 1932 and 1939. He moved to the United States and became a naturalized citizen. He was a research associate in respiratory physiology at Swarthmore College in Swarthmore, Pennsylvania, from 1939 to 1943. He was a Rockefeller fellow from 1939 to 1941 and a research biologist from 1946 to 1949. He was a major for the U.S. Army Air Force Research from 1943 to 1946, and during this time was chief physiologist test officer, Air Force Base, Eglin Field near Valparaiso, Florida (1943–1945), and an aviation physiologist at the aeromedical laboratory of Wright Field, Dayton, Ohio (1945–1946).

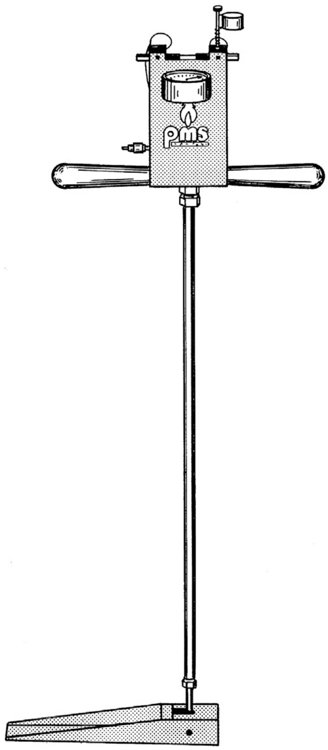

FIGURE 19.10 Overall view of the pump-up pressure chamber, an alternative type of pressure chamber that does not use compressed gas. *From a PMS Instrument Company, Corvallis, Oregon, brochure. Reprinted by permission of PMS Instrument Company.*

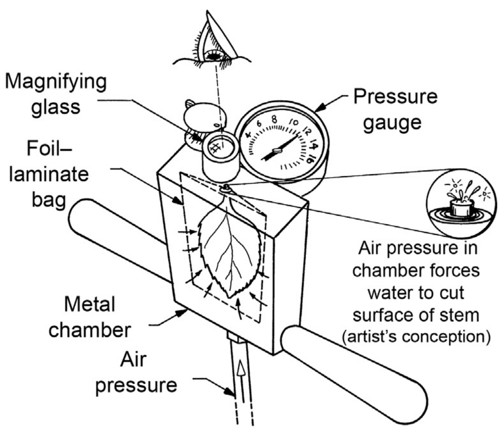

FIGURE 19.11 A close-up of the top part of the pump-up pressure chamber. *From a PMS Instrument Company, Corvallis, Oregon, brochure. Reprinted by permission of PMS Instrument Company.*

From 1949 to 1951, he was a special research fellow in biochemistry at Harvard Medical School. He was a physiologist at the Oceanographic Institute in Woods Hole, Massachusetts, between 1952 and 1955. In 1955, he returned to Oslo, where he was a professor of physiology and director of the institute of zoophysiology until 1958. During this time (1955–1958) he also was an associate at the Oceanographic Institute in Woods Hole. In 1958, he became a professor of physiology at the Scripps Institute of Oceanography in La Jolla, California, where he spent the rest of his career.

His honors included being an investigator in the Arctic Research Laboratory of the Office of Naval Research in Alaska and Panama from 1947 to 1949. He was a member of the polar research committee of the National Academy of Sciences and participated in arctic and tropical expeditions. He received the Legion of Merit in 1946. He was a member of the National Academy of Sciences, American Association for the Advancement of Science, Physiology Society, Society of Zoologists, Society of Plant Physiologists, Society of General Physiology, American Academy, Arctic Institute of North America, Norwegian Academy of Science, Norwegian Physiology Society, and Botanical Association of Norway. His major research areas were arctic botany, respiration of diving, cold adaptation, microtechniques, gas secretion, water and gas transport in plants, and gas in glaciers (American Men of Science, 1961).

According to the *Newsletter of the American Society of Plant Physiologists* (vol. 7, No. 5, p. 4, October, 1980), Per Scholander died June 13, 1980, at the age of 74.

19.6 APPENDIX: BIOGRAPHY OF JOHN BOYER

John Strickland Boyer, a biochemist and biophysicist, was born May 1, 1937, in Cranford, New Jersey (Marquis Who's Who, 2000). He married Jean R. Matsunami and they have two children. In 1961 he got his master's degree at the University of Wisconsin under the direction of Gerald C. Gerloff, a mineral nutritionist, and in 1964 he obtained his PhD in botany at Duke University under the direction of Paul J. Kramer. The last book by Kramer was written jointly with Boyer (Kramer and Boyer, 1995). (Paul Kramer was born May 8, 1904, and died May 24, 1995.)

Boyer was visiting assistant professor of botany at Duke University from 1964 to 1965, and an assistant physiologist at the Connecticut Agricultural Experiment Station during 1965–1966. In 1966 he moved to the University of Illinois at Urbana and rose from assistant professor to professor of botany and agronomy. In 1978, he joined the U.S. Department of Agriculture (USDA) as a plant physiologist on the University of Illinois campus. Between 1984 and 1987 he was a professor at Texas A&M University. In 1987 he became the du Pont Professor of Marine Biochemistry and Biophysics at the University of Delaware. He retired from the faculty on June 30, 2005, and is now E.I. du Pont Professor of Biochemistry and Biophysics Emeritus at the University of Delaware (Chell, 2013).

He has won many recognitions. He is a member of the visitor committee, Carnegie Institute of Washington, Stanford University, and Harvard University. In 1983, he received the German Humboldt Senior Scientist award. He is a fellow of the Climate Laboratory (New Zealand), American Society of Agronomy, Crop Science Society of America, Australian National University, and the Japanese Society for the Promotion of Science. In 1990, he was elected member of the U.S. National Academy of Sciences. In 2005, he was elected a corresponding member of the Australian Academy of Science. He is a member of the American Society of Plant Physiologists (now called the American Society of Plant Biologists) and was president of the society in 1981–1982. He won the society's Shull award in 1977 (Marquis Who's Who, 2000).

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