Problems Associated with Measuring Plant Water Status

Jerry M. Bennett

*Department of Agronomy, Institute of Food and Agricultural Sciences, University of Florida,
Gainesville, FL 32611*

The water status of plant cells affects physiological and metabolic activities as well as expansion and growth. Accurate measurements of plant water status are essential for a better understanding of productivity under various environmental conditions. Numerous measurement techniques have proven useful for improving our understanding of how plants respond to water deficits. It is beyond the scope of this presentation to describe all of the methods used for measuring plant water status or to fully address all problems associated with even the most common methods. Rather, the purpose of this paper is to discuss some advantages, disadvantages, and problems associated with the more commonly used techniques. I hope that pointing out potential errors and necessary precautions will challenge readers to review the excellent published papers dealing with specific topics. References cited herein represent only a small fraction of the papers that address the measurement of plant water status but will serve to illustrate the breadth of the literature.

TECHNIQUES FOR MEASURING PLANT WATER STATUS

This discussion will focus on the following techniques that have been used to measure plant water status: Determination of relative water content, hydraulic press, thermocouple psychrometers, leaf in situ psychrometers, pressure chamber, and pressure probe. Obviously, all of the methods currently in use cannot be covered in detail. Readers are referred to Kramer (1974, 1983), Turner (1981, 1986b, 1987) and Kirkham (1985) for more detailed information on the techniques summarized below.

Relative water content

Relative water content is a measure of the actual water content of a tissue with reference to the content of water in the tissue if it were fully hydrated. Determination of relative water content is simple and does not require expensive equipment. Measurement of relative water content involves obtaining three measurements made on the same sample: fresh weight, turgid weight, and dry weight. Fresh weight of the sample is determined immediately after the tissue is excised from the plant, turgid weight is determined after the tissue has equilibrated with pure water and attained full turgid-

ity, and dry weight of the tissue is determined after oven drying. Percent relative water content (RWC) is then expressed as: $\% \text{ RWC} = (\text{fresh wt.} - \text{dry wt.} / \text{turgid wt.} - \text{dry wt.}) \times 100$.

Some of the precautions that must be considered when measuring relative water content include the following: a) Surface water must be completely removed from the tissue before determining fresh or turgid weights; b) care must be taken to avoid loss of water after tissue excision and before determination of fresh weight; c) measurements of tissue weights are best made under laboratory conditions, but fresh samples may be transported short distances from a field to a laboratory if precautions to prevent water loss from samples are taken; d) tissue respiration may result in loss of dry weight during the equilibration period required for attaining turgid weight; low-intensity illumination is sometimes used to compensate for respiration losses; e) infiltration of water into cut edges of sampled tissue may result in turgid weight errors; f) slow water uptake may continue as a result of growth during equilibration (Barrs and Weatherly, 1962), making it difficult to determine the time required to attain full turgor. Length of time required for tissues to obtain turgid weights may vary depending on plant species and may be quite long for some plants; g) the relationship between relative water content and water potential may change with plant age, plant part, season or species (Slatyer, 1967).

Hydraulic press

Use of a hydraulic press involves application of pressure from beneath a flexible membrane to a leaf that is positioned between the membrane and a plexiglass plate. Water is expressed from the leaf tissue as pressure is increased. The pressure at which water is initially expressed from the tissue (or when the tissue appears water-soaked) has been used by some researchers as an indication of the leaf water potential.

Researchers using the hydraulic press as a measure of plant water status should consider the following: a) Use of the hydraulic press is convenient, rapid, and well-adapted for field and greenhouse conditions, but results may not be accepted by all researchers as an accurate indication of plant water status; b) some studies have shown good correlation between measurements made with the hydraulic press and leaf water potentials determined with thermocouple psychrometers or pressure chambers (Rajendrudu et al., 1983), while other studies have shown poor agreement between hydraulic press

measurements and leaf water potentials measured with more readily accepted techniques (Bristow et al., 1981; Sojka et al., 1987). Therefore, calibration of data from the hydraulic press with measurements from either a pressure chamber or thermocouple psychrometers is recommended for each specific tissue examined; c) determination of the endpoint is often indefinite and subject to misinterpretation in some species.

Thermocouple psychrometers

Thermocouple psychrometers have been used by many researchers to determine both water and osmotic potentials of plant tissues. Most thermocouple psychrometers consist of a chromel-constantan sensing junction that is used as a wet bulb to determine the equilibration vapor pressure above a sample of plant tissue (Brown and Collins, 1980). Along with the pressure chamber, thermocouple psychrometers have been used more than any other technique for measuring plant water status. Numerous papers have been published dealing with the use of thermocouple psychrometers (Bayer, 1972; Boyer and Knipling, 1965; Brown and Collins, 1980; Meyn and White, 1972; Millar, 1982; Oosterhuis and Wullschlegel, 1987; Rawlins, 1966; Turner, 1981; Walker et al., 1983) and symposia to discuss their use in plant water relations have been conducted (Brown and Van Haveren, 1972).

Major items to consider when using thermocouple psychrometers include: a) accurate measurement of water status using thermocouple psychrometers requires a stable temperature environment for equilibration and measurement; b) accurate measurements require use of a microvoltmeter, strip chart recorder, and often a temperature-controlled water bath; c) measurement of thermocouple psychrometer output is generally a laboratory technique and requires that samples be transported from the field or greenhouse to a stable temperature environment for equilibration and measurement; d) changes in the water potential components of the plant tissue may occur during the somewhat lengthy periods often required for vapor and temperature equilibration (Bennett et al., 1986; Grange, 1983); e) cut edge effects may cause errors when using small samples of plant material (Barrs and Kramer, 1969; Bennett and Cortes, 1985); f) water and turgor potentials of plant tissue may decline significantly if tissue expansive growth continues during the equilibration period (Van Volkenburgh and Cleland, 1986); g) heat from tissue respiration may result in errors if the sample and thermocouple sensing junction are not at the same temperature (Barrs, 1964); h) only a limited number of samples can be equilibrated at one time; i) errors may result from samples having high tissue resistance to water vapor movement when using Spanner- or Richards-type thermocouple psychrometers (Boyer, 1972; Boyer and Knipling, 1965; Shackel, 1984); use of isopiestic thermocouple psychrometers has been shown to overcome the problem of large tissue resistances to water vapor (Boyer, 1972; Boyer and Knipling, 1965); j) use of thermocouple psychrometers is rather time-consuming and requires skillful calibration; k) water adsorption by psychrometer chamber walls, especially if constructed of certain types of materials, and other vapor sinks may lead to errors (Bennett and Cortes, 1985; Boyer, 1972; Campbell, 1972; Dixon and Grace, 1982); l) care must be taken to prevent water loss from the tissue after excision and before sealing into the psychrometer chamber (Oosterhuis and Wullschlegel, 1957); m) it is important to determine equilibration times for different tissues and plant species (Talbot et al., 1976; Walker et al., 1983); n) thermocouple psychrometers may be used to estimate both leaf water and osmotic potential, although some obvious and potentially serious errors may result in the measure of osmotic potential of some species (Bennett et al., 1986; Grange, 1983; Turner, 1981). Freezing and thawing of tissue or expression of cell sap from the tissue is necessary before osmotic potential can be determined. Dilution of cell sap by apoplastic water may occur after freezing and thawing, resulting in a higher (less negative) osmotic potential than in the intact tissue. In contrast, formation of osmotically active compounds during equilibration may result in lower (more negative) osmotic potentials than those in the intact tissue.

Leaf in situ hygrometers

Leaf in situ hygrometers provide the opportunity to monitor the dynamic changes in plant water potential continuously (Campbell and Campbell, 1974; McBurney and Costigan, 1987; Shackel and Brinckmann, 1985). However, use of in situ hygrometers for measuring leaf water potential in field or even greenhouse environments has inherent problems, most of which relate to temperature gradients that are extremely difficult to control. Recent research has led to improvements in design of in situ hygrometers and some designs have been shown to alleviate some of the temperature gradient problems. Nevertheless, temperature gradients remain as the primary problem associated with in situ hygrometers.

Those interested in using in situ hygrometers should consider the following: a) Abrasion of the leaf cuticle may be required to facilitate rapid vapor exchange between the plant tissue and the psychrometer atmosphere; b) requirements for temperature stability generally limit the use of in situ hygrometers to controlled environments, although some progress has recently been made to stabilize temperatures in field and greenhouse environments (McBurney and Costigan, 1987; Savage et al., 1983; Turner et al., 1984); c) the number of samples that can be measured at any one time is limited; d) as with any thermocouple psychrometer, in situ psychrometers require somewhat expensive read-out equipment and must be carefully calibrated.

Pressure chamber

The pressure chamber has become widely accepted as an instrument that is well-adapted for measurement of leaf water potential in a variety of plant species (Schoiander et al., 1965). Pressure is applied to excised leaf tissue until the xylem water is returned to the cut end of the petiole. An excellent review by Ritchie and Hinckley (1976) addressed the use of the pressure chamber in ecological studies. Those interested in the use of pressure chambers for measurement of plant water status should consider the following: a) A pressure chamber is easy to use and allows measurement of a large number of samples in a short period of time; b) a pressure chamber is portable and well-adapted to field or greenhouse environments; c) Calibration of results obtained with a pressure chamber to leaf water potentials measured with thermocouple psychrometers may be necessary and has been accomplished for various species (Blum et al., 1973; Boyer, 1967; De Roo, 1969; Grant et al., 1981; Kaufmann, 1968; Kikuta et al., 1985; Ritchie and Hinckley, 1976; Turner, 1987; Turner et al., 1984; West and Gaff, 1971); although agreement between water potentials measured with thermocouple psychrometers and pressure chambers is often good, considerable discrepancies may exist for some species; d) a pressure chamber can be used to generate pressure-volume curves for plant tissues (Kandiko et al., 1980; Turner, 1987; Tyree and Hammel, 1972); e) Purchase and use of a pressure chamber is relatively inexpensive; f) Damage to leaf tissue may occur in a pressure chamber, especially at high pressures; g) the pressure chamber has become commonly accepted as an accurate technique for measuring plant water potential; h) water loss from the leaf must be minimized after excision from the plant. Large errors can occur if leaf tissue is left exposed to a drying atmosphere for even short periods of time (Allen et al., 1980; Meyer and Reicosky, 1985; Turner, 1987; Turner and Long, 1980); failure to prevent water loss from excised leaves is probably the largest source of error in the use of a pressure chamber, especially in field and greenhouse studies where significant changes in water potential can occur soon after leaf excision; enclosing the leaf in a plastic, humidified sheath immediately before excision has been shown to reduce water loss significantly (Turner and Long, 1980); i) accurate endpoints are sometime difficult to determine. The difficulty of accurately determining the exact endpoint seems to be both cultivar- and species-dependent, and may be complicated by excretion of latex and resins in some tissues; j) measurement of leaf water potential with a pressure chamber does not include the osmotic potential of the xylem sap, although concentrations of solutes in xylem water are generally low in most plants; however, in certain species, significant osmotic potential may exist in the xylem stream

(Boyer, 1967); k) recutting the petiole after initial excision should be avoided (Turner, 1981); l) the chamber should be slowly pressurized for accurate measurement of leaf water potential (Blum et al., 1973); m) the pressure chamber has been adapted for pressurizing root systems to increase the turgor of shoots for studying the effects of drying soil independently from effects of changes in shoot turgidity (Passioura, 1987).

Pressure probe

The pressure probe is a relatively new technique that is used to measure turgor potential directly in individual living cells (Frensch and Schulze, 1987; Husken et al., 1978; Shackel and Brinckmann, 1985; Stuedle, 1987). A miniature probe is inserted into a plant cell and the internal cell pressure is transmitted to a pressure transducer through an oil-filled microcapillary (Husken et al., 1978). Information gained through use of this technique will likely continue to make significant contributions to our understanding of cellular water relations. Those interested in using the pressure probe should be aware that: a) The pressure probe provides an accurate method for directly measuring cell turgor; b) the use of a pressure probe is rather tedious, is limited to laboratory environments, and provides a measure of turgor of individual cells rather than average bulk turgor of tissues; c) use is limited to larger cells that are easily penetrable; d) currently, the pressure probe has not been successfully used to determine turgor potential in guard cells because of plugging of the probe upon insertion; e) use of the pressure probe requires skill and expertise for successful use.

RELATION OF PLANT WATER STATUS TO PHYSIOLOGICAL ACTIVITY

The status of our understanding of how water stress affects plant physiological processes, growth, and productivity has been reviewed in several excellent papers (Kramer, 1974, 1983; Schulze, 1986; Turner, 1986a, 1986b). Data from recent studies reemphasize that our understanding of exactly which plant characters should be measured at what intervals in order to define plant water stress accurately is incomplete. As an example, numerous authors have recently demonstrated that the link between stomatal activity and bulk leaf water status is not straightforward (Bates and Hall, 1981; Bennett et al., 1987; Black et al., 1985; Davies et al., 1986; Shackel and Brinckmann, 1985; Sinclair and Ludlow, 1985; Turner, 1986a). Some authors (Sinclair and Ludlow, 1985) have argued that the thermodynamic properties of water may not be the signals to which plants respond directly and have suggested that relative water content might be a better measure of plant water status. However, other studies have shown stomatal conductance to be poorly correlated with bulk leaf relative water content (Bennett et al., 1987). The lack of unique relationships among leaf water potential, leaf turgor potential, and relative water content with stomatal conductance (or photosynthesis), which has been observed in many studies, suggests that other interacting factors cannot be ignored. Indeed, the relationships between physiological activities of plants with currently used and accepted measures of plant water status are often not as clear as desired. Possibly, past research in plant water relations has placed too much emphasis on the responses of severely stressed plants while ignoring the physiological changes that occur in plants that are only mildly stressed.

Recent research has begun focusing on the role of plant growth regulators that may move from roots to shoots and alter the physiology of plant shoots independently of leaf water status when roots are subjected to drying soil (Blackman and Davies, 1985; Davies et al., 1986; Schulze, 1986; Turner, 1986a, 1986b). Turner (1986a) has suggested that more emphasis be placed on roots as opposed to shoots as the sensors of soil water deficits. Clearly, more research should be directed to developing approaches and techniques to define soil and plant water deficits more accurately. Many difficult but stimulating challenges remain and novel approaches will be required to better understand the signals to which plants respond during periods of limiting soil water.

Literature Cited

- Allen, J.J., T.A. Nell, J.N. Joiner, and L.G. Albrigo. 1980. Effects of leaf position and storage conditions on pressure bomb measurement of leaf water potential in chrysanthemums. *HortScience* 15:808-809.
- Bans, H.D. 1964. Heat of respiration as a possible cause of error in the estimation by psychrometric methods of water potential in plant tissue. *Nature (London)* 203:1136-1137.
- Bans, H.D. and P.J. Kramer. 1969. Water potential increase in sliced leaf tissue as a cause of error in vapor phase determinations of water potential. *Plant Physiol.* 44:959-964.
- Bans, H.D. and P.E. Weatherly. 1962. A reexamination of the relative turgidity technique for estimating water deficits in leaves. *Austral. J. Biol. Sci.* 15:413-428.
- Bates, L.M. and A.E. Hall. 1981. Stomatal closure with soil water depletion not associated with changes in bulk leaf water status. *Oecologia* 50:62-65.
- Bennett, J.M. and P.M. Cortes. 1985. Errors in measuring water potentials of small samples resulting from water adsorption by thermocouple psychrometer chambers. *Plant Physiol.* 79:184-188.
- Bennett, J.M., P.M. Cartes, and G.F. Lorens. 1986. Comparison of water potential components measured with a thermocouple psychrometer and a pressure chamber and the effects of starch hydrolysis. *Agron. J.* 78:239-244.
- Bennett, J.M., T.R. Sinclair, R.C. Muchow, and S.R. Costello. 1987. Dependence of stomatal conductance on leaf water potential, turgor potential, and relative water content in field-grown soybean and maize. *Crop Sci.* 27:984-990.
- Black, C.R., D.-Y. Tang, C.K. Ong, A. Solon, and L.P. Simmonds. 1985. Effects of soil moisture stress on the water relations and wafer use of groundnut stands. *New Phytol.* 100:313-328.
- Blackman, P.G. and W.J. Davies. 1985. Root to shoot communication in maize plants and the effects of soil drying. *J. Expt. Bot.* 36:39-48.
- Blum, A., C.Y. Sullivan, and J.D. Eastin. 1973. On the pressure chamber technique for estimating leaf water potential in sorghum. *Agron. J.* 65:337-338.
- Boyer, J.S. 1967. Leaf water potentials measured with a pressure chamber. *Plant Physiol.* 42:133-137.
- Boyer, J.S. 1972. Use of isopiestic technique in thermocouple psychrometry. II. Construction, p. 51-55. In: R.W. Brown and B.P. Van Haveren (eds.). *Psychrometry in water relations research*. Utah Agr. Expt. Sta., Utah State Univ., Logan.
- Boyer, J.S. and E.B. Knippling. 1965. Isopiestic technique for measuring leaf water potentials with a thermocouple psychrometer. *Proc. Natl. Acad. Sci.* 54:1044-1051.
- Bristow, K.L., W.H. van Zyl, and J.M. de Jager. 1981. Measurement of leaf water potential using the J14 press. *J. Expt. Bot.* 32:851-854.
- Brown, R.W. and J.M. Collins. 1980. A screen-caged thermocouple psychrometer and calibration chamber for measurements of plant and soil water potential. *Agron. J.* 72:851-854.
- Brown, R.W. and B.P. Van Haveren (eds.). 1972. *Psychrometry in water relations research*. Utah Agr. Expt. Sta., Utah State Univ., Logan.
- Campbell, E.C. 1972. Vapor sink and thermal gradient effects on psychrometer calibration, p. 94-97. In: R.W. Brown and B.P. Van Haveren (eds.). *Psychrometry in water relations research*. Utah Agr. Expt. Sta., Utah State Univ., Logan.
- Campbell, G.S. and M.D. Campbell. 1974. Evaluation of a thermocouple hygrometer for measuring leaf water potential in situ. *Agron. J.* 66:24-27.
- Davies, W.J., J. Metcalfe, T.A. Lodge, and A.R. da Costa. 1986. Plant growth substances and the regulation of growth under drought. *Austral. J. Plant Physiol.* 13:105-125.
- De Roo, H.C. 1969. Leaf water potentials of sorghum and corn, estimated with the pressure bomb. *Agron. J.* 61:969-970.
- Dixon, M. and J. Grace. 1982. Water uptake by some chamber materials. *Plant, Cell & Environ.* 5:323-327.
- Frensch, J. and E.-D. Schulze. 1987. Methods of determining gradients in tissue water relation parameters and their effect on stomatal behavior. vol. 2. *Intl. Conf. on measurement of Soil and Plant Water Status*. Utah State Univ., Logan. p. 147-154.
- Grange, R.I. 1983. Solute production during the measurement of solute potential of disrupted tissue. *J. Expt. Bot.* 34:757-764.
- Grant, R.F., M.J. Savage, and J.D. Lea. 1981. Comparison of hydraulic press, thermocouple psychrometer, and pressure chamber for the measurement of total and osmotic leaf water potential in soybeans. *S. Afr. J. Sci.* 77:398-400.
- Husken, D., E. Stuedle, and U. Zimmerman. 1978. Pressure probe tech-

- nique for measuring wafer relations of cells in higher plants. *Plant Physiol.* 61:158-163.
- Kandiko, R.A., R. Timmis, and J. Worrall. 1980. Pressure-volume curves of shoots and roots of normal and drought conditioned western hemlock seedlings. *Can. J. For. Res.* 10:10-15.
- Kaufmann, M.R. 1968. Evaluation of the pressure chamber technique for estimating plant water potential of forest tree species. *For. Sci.* 14:369-374.
- Kikuta, S.B., E. Kyriakopoulos, and H. Richter. 1985. Leaf hygrometer v. pressure chamber: a comparison of pressure-volume curve data obtained on single leaves by alternating measurements. *Plant Cell & Environ.* 8:363-367.
- Kirkham, M.B. 1985. Techniques for water-use measurements of crop plants. *HortScience* 20:993-1001.
- Kramer, P.J. 1974. Fifty years of progress in water relations research. *Plant Physiol.* 54:463-371.
- Kramer, P.J. 1983. Water relations of plants. Academic, New York.
- McBurney, T. and P.A. Costigan. Plant water potential measured continuously in the field. *Plant and Soil* 97:145-149.
- Meyer, W.S. and D.C. Ricosky. 1985. Enclosing leaves for water potential measurement and its effect on interpreting soil-induced water stress. *Agr. For. Met.* 35:187-192.
- Meyn, R.L. and R.S. White. 1972. Calibration of thermocouple psychrometers: a suggested procedure for development of a reliable predictive model. p. 56-63. In: R.W. Brown and B.P. Van Haveren (eds.). *Psychrometry in water relations research*. Utah Agr. Expt. Sta., Utah State Univ., Logan.
- Millar, B.D. 1982. Accuracy and usefulness of psychrometer and pressure chamber for evaluating water potentials of *Pinus radiata* needles. *Austral. J. Plant Physiol.* 9:499-507.
- Oosterhuis, D.M. and S.D. Wullschlegel. 1987. The use of leaf discs in thermocouple psychrometers for measurement of water potential. vol. 2. Intl. Conf. on Measurement of Soil and Plant Water Status. Utah State University, Logan. p. 77-81.
- Passioura, J.B. 1987. The use of the pressure chamber for continuously monitoring and controlling the pressure in the xylem sap of the shoot of intact transpiring plants. vol. 2. Intl. Conf. on Measurement of Soil and Plant Water Status. Utah State Univ. Logan. p. 31-34.
- Rajendrudu, G., M. Singh, and J.H. Williams. 1983. Hydraulic press measurements of leaf water potential in groundnuts. *Expt. Agr.* 19:287-291.
- Rawlins, S.L. 1966. Theory for thermocouple psychrometers used to measure water potential in soil and plant samples. *Agr. Met.* 3:293-310.
- Ritchie, G.A. and T.M. Hinckley. 1976. The pressure chamber as an instrument for ecological research. *Adv. Ecol. Res.* 9:165-254.
- Savage, M.J., H.H. Wiebe, and A. Cass. 1983. In situ field measurement of leaf water potential using thermocouple psychrometers. *Plant Physiol.* 73:609-613.
- Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* 148:339-346.
- Schulze, E.-D. 1986. Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. *Annu. Rev. Plant Physiol.* 37:247-274.
- Shackel, K.A. 1984. Theoretical and experimental errors for in situ measurements of plant water potential. *Plant Physiol.* 75:766-772.
- Shackel, K.A. and E. Brinckmann. 1985. In situ measurement of epidermal cell turgor, leaf water potential, and gas exchange in *Tradescantia virginiana* L. *Plant Physiol.* 78:66-70.
- Sinclair, T.R. and M.M. Ludlow. 1985. Who taught plants thermodynamics? The unfulfilled potential of plant water potential. *Austral. J. Plant Physiol.* 12:213-217.
- Slatyer, R.O. 1967. *Plant water relationships*. Academic, New York.
- Sojka, R.E., E.J. Sadler, C.R. Camp, and F.B. Arnold. 1987. Comparison of Campbell leaf-press with standard plant water stress measurements for four species. Intl. Conf. on Measurement of Soil and Plant Water Status. Utah State Univ. Logan. p. 39-45.
- Stuedle, E. 1987. Pressure probe techniques: some recent developments. Intl. Conf. on Measurement of Soil and Plant Water Status. Utah State Univ. Logan. p. 183-191.
- Talbot, A.J.B., M.T. Tyree, and J. Dainty. 1976. Some notes concerning the measurement of water potentials of leaf tissue with specific reference to *Tsuga canadensis* and *Picea abies*. *Can. J. Bot.* 53:784-788.
- Turner, N.C. 1981. Techniques and experimental approaches for measurement of plant water status. *Plant and Soil* 58:339-366.
- Turner, N.C. 1986a. Adaptation to water deficits: a changing perspective. *Austral. J. Plant Physiol.* 13:174-190.
- Turner, N.C. 1986b. Crop water deficits: a decade of progress. *Adv. Agron.* 39:1-51.
- Turner, N.C. 1987. The use of the pressure chamber in studies of plant water status. Intl. Conf. on Measurement of Soil and Plant Water Status. Utah State Univ., Logan. p. 13-24.
- Turner, N.C. and M.J. Long. 1980. Errors arising from rapid water loss in the measurement of leaf water potential by the pressure chamber technique. *Austral. J. Plant Physiol.* 7:527-537.
- Turner, N.C., R.A. Spunvay, and E.-D. Schulze. 1984. Comparison of water potentials measured by in situ psychrometry and pressure chamber in morphologically different species. *Plant Physiol.* 74:316-319.
- Tyree, M.T. and H.T. Hammel. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *J. Expt. Bot.* 23:267-282.
- Van Volkenburgh, E. and R.E. Cleland. 1986. Wall yield threshold and effective turgor in growing bean leaves. *Planta* 167:37-43.
- Walker, S., D.M. Oosterhuis, and M.J. Savage. 1983. Field use of screen-caged thermocouple psychrometers in sample chambers. *Crop Sci.* 23:627-632.
- West, D.W. and D.F. Gaff. 1971. An error in the calibration of xylem-water potential against leaf-water potential. *J. Expt. Bot.* 22:342-346.