Chapter 5

Measuring the Water Status of Plants and Soils: Some Examples

In order to help the reader design experiments for measuring the water status of plants and soils, this chapter describes a few examples that illustrate in a practical way the kinds of information that can be gained. The examples are taken from the original literature and represent only a partial sampling. For a fuller account the reader is directed to Kramer and Boyer (1995).

Practical Benefits of Thermodynamic Equilibrium

In the previous chapters, emphasis was placed on measuring the water status at thermodynamic equilibrium. The practical benefit can be seen in comparative studies of sorghum leaves made by De Roo (1969) using equilibrium methods and Blum *et al.* (1973) using similar methods but not operated at equilibrium. De Roo (1969) compared the water potential measured with an isopiestic psychrometer and the xylem pressure measured at balance in a pressure chamber and found them to be virtually equivalent, i.e., close to the line of equivalency shown in Fig. 5.1A. De Roo (1969) also determined the osmotic potential of the xylem solution and found it to be on average -0.05 MPa. Adding this potential to the xylem pressure in Fig. 5.1A gives the leaf water potential (see Chap. 2) and an even closer correspondence to the equivalency line. Note that there was little variation in the data. Because the data fall on the line of equivalency, there is no uncertainty about which method is correct and no need to calibrate. The pressure chamber compares so well with the psychrometer, which has already been shown to give absolute values of the water potential (see Chap. 3), that both methods can be considered to give absolute values of the water potential of sorghum leaves.

Blum *et al.* (1973) also studied sorghum leaves but in contrast to De Roo (1969) used the pressure chamber as a nonequilibrium method by noting the first appearance of xylem solution when the sample was pressurized at a constant rate (Figs. 5.1B and 5.1C). A comparison was made with thermocouple psychrometer readings by the

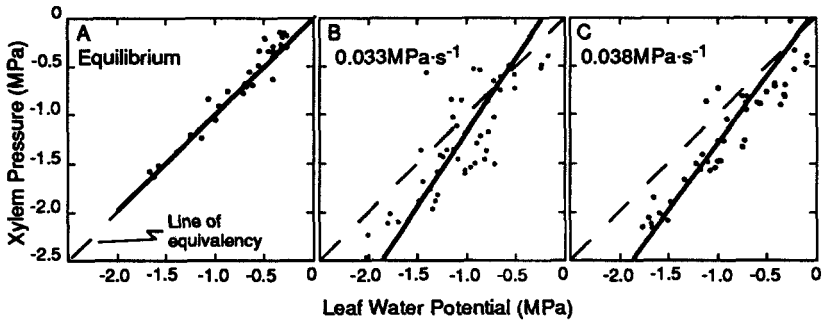

Figure 5.1. Comparison of the water status of sorghum leaves measured with a psychrometer and a pressure chamber. A) Leaf water potential determined with an isopiestic thermocouple psychrometer and compared with the xylem pressure at balance in the same leaf. These are equilbrium methods. The line of equivalency (dashed line) indicates a 1:1 correspondence between them. Data from De Roo (1969). B) The same comparison using a Peltier psychrometer for leaf water potential and a pressure chamber pressurized at a steady rate (0.033 MPa·sec^{-1}) for xylem pressure. These are not equilibrium methods. Data from Blum *et al.* (1973). C) As in B except the pressure chamber was pressurized more rapidly (0.038 MPa·sec^{-1}). Data from Blum *et al.* (1973).

Peltier method which also is not an equilibrium technique. It is clear that the data do not match the line of equivalency and that the relation depends on the rate of pressure application (cf. Figs. 5.1B and 5.1C). Also, the data show a large variability. Blum *et al.* (1973) indicate that if one uses nonequilibrium methods, careful calibration is essential. They also point out that it is not clear whether the pressure chamber or psychrometer gives the more accurate values. Therefore, one may consider the nonequilibrium data to be only relative approximations. Clearly, the equilibrium techniques used by De Roo (1969) are preferred. Their freedom from calibration and lack of variability are desirable features, and the ability to interpret the measurements is simplified by having absolute values of the potential.

Large Tensions Demonstrated in the Apoplast

Scholander *et al.* (1965) interpreted their pressure chamber measurements as a demonstration that large tensions exist in the xylem

and apoplast of plants. Large tensions are easily disrupted because water is in a quasi-stable state and water columns can break because of cavitation. As a consequence, doubts are sometimes expressed that such large tensions can exist, and indeed attempts to demonstrate large tensions sometimes fail (see Kramer and Boyer, 1995 for some recent examples). This is especially true when the xylem is penetrated with a pressure probe because the penetration itself can disrupt the water column by causing cavitation. On the other hand, the psychrometer measures the water potential directly in the apoplast and does not penetrate the water column. As shown by De Roo (1969), the osmotic potential of the apoplast solution was only -0.05 MPa in sorghum and the only other possible potential is a tension (part of $\Psi_{m(a)}$ in Eq. 2.4 and Fig. 2.4B). Therefore, the low water potentials in the apoplast (Fig. 5.1A) are strong evidence supporting the interpretation that large tensions exist.

It should be noted that the isopiestic psychrometer is the only method shown to give accurate absolute values of the water potential using plant tissue of known water potential (see Fig. 3.7). Leaves on intact plants have water potentials similar to the water potentials of excised samples from the same leaves (Boyer, 1968). Therefore, excision does not alter the conclusions, and the tensions have been demonstrated in many species using the isopiestic psychrometer and the pressure chamber (Boyer, 1967a; Ghorashy *et al.*, 1971; De Roo, 1969).

Single Cell and Tissue Measurements Compared

Figure 5.2 compares the variation in turgor in cells measured with a miniature pressure probe and in tissues grown identically and measured with an isopiestic psychrometer (Nonami *et al.*, 1987). Mature tissue was used from stems of soybean seedlings after transplanting to vermiculite of low water content, and it is apparent that the turgor initially decreased (Fig. 5.2A), then increased as recovery occurred without rewatering when the roots reconnected with the water supply (Fig 5.2B).

The variability was greater among individual cells (pressure probe) than among the tissue samples (psychrometer). For the cells, the variation included differences among plants and among cells of the same plant, and perhaps some variation attributable to the probe. For the tissues, many cells contributed to each tissue sample and four to six

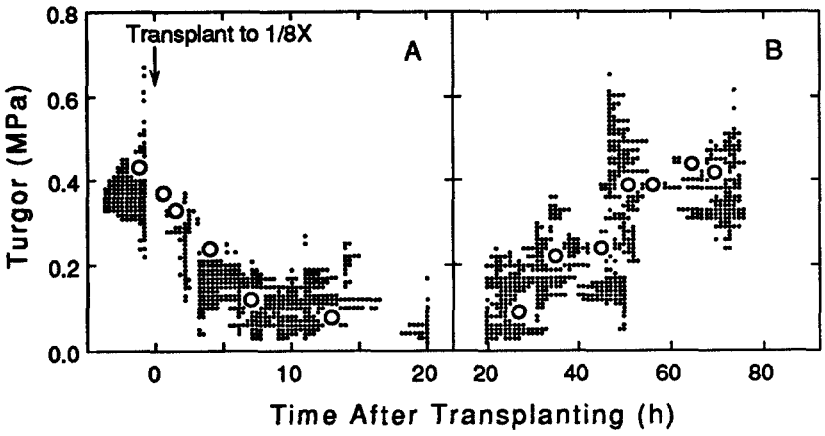

Figure 5.2. Turgor pressures measured in the mature region of soybean stems using a miniature pressure probe (small points) and an isopiestic thermocouple psychrometer (open circles). Pressure probe data are for individual cells of the intact plant, psychrometer data are for excised tissue segments. A) The soybean seedlings were transplanted to vermiculite of low water content at 0 hr whereupon turgor fell for 15 hr. B) Twenty hours after transplanting, turgor recovered because the roots reconnected with the water supply. Each data point is an individual measurement. From Nonami *et al.* (1987).

plants were represented in each measurement to give an average. This illustrates that there is no substitute for individual cell data when one is exploring cell properties, but there is less labor with the psychrometer (or pressure chamber) when measuring the water status of tissues. The psychrometer gives simultaneous averages for all the cells, which is not possible with the pressure probe.

It is noteworthy that the two methods agree because they rely on different principles of measurement. The agreement gives confidence in the results, and it appears that penetrating the cells with the microcapillary and excising the mature tissue for the psychrometer do not disturb the turgor significantly. A comparison of tissue turgor also has been made with sunflower leaves using a pressure chamber at balance and an isopiestic psychrometer (Boyer and Potter, 1973) and gave similar results provided a correction was made for dilution of the cell solution by apoplast solution during the measurement with the

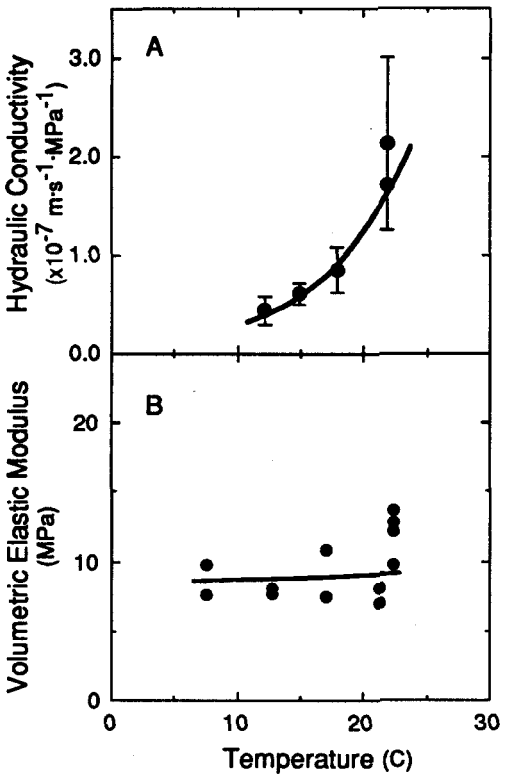

Figure 5.3. Temperature response of (A) hydraulic conductivity and (B) volumetric elastic modulus in *Tradescantia* epidermal cells. Measurements were made with a miniature pressure probe. Data from Tomos *et al.* (1981).

psychrometer (see Chap. 3). With the correction, the osmotic potentials were similar for the two methods (Boyer and Potter, 1973).

Temperature, Membrane Transport, and Cell Walls

Biological activity depends on enzyme reactions that are markedly responsive to temperature, and the movement of ions and metabolites across membranes varies with temperature in part because of the involvement of enzyme reactions in their transport. By contrast, water moves passively into cells, driven by differences in potential on the two sides of the plasmalemma, as can be demonstrated readily with a pressure chamber or pressure probe. For strictly passive transport

through a membrane, water would be expected to move slightly more rapidly as temperatures rise and the viscosity of water decreases moderately. However, Fig. 5.3A shows that the hydraulic conductivity of *Tradescantia* cells increases about 5-fold as the temperature rises to 22°C from 12°C (Tomos *et al.*, 1981) and is more like the thermal response of an enzymatic reaction than the viscosity, which changes only 1.3-fold. A possible explanation is that pore-forming proteins appear to be involved in water transport (Kramer and Boyer, 1995), and protein synthesis and insertion into the membrane might influence membrane conductivity because these processes are highly responsive to temperature.

Likewise, the cell wall is synthesized by metabolic reactions that are temperature-dependent but the wall elasticity is a physical property whose temperature response is difficult to predict. Tomos *et al.* (1981) showed that the volumetric elastic modulus of the wall is virtually constant at various temperatures in *Tradescantia* (Fig. 5.3B). The modulus is used to calculate the hydraulic conductivity of membranes for water (see Chap. 4), but this result indicates that the modulus is not the cause of the large conductivity response to temperature.

Importance of Growth

Plants grow mostly by enlarging the cells produced in meristems. The enlargement requires water uptake and some solute transport, and excising the tissues disrupts both processes. The psychrometer for intact plants does not suffer from this problem and is the only method that completely maintains the integrity of tissues and cells (see Chap. 3). The method has been used to study the growth process (Boyer, 1968; Boyer *et al.*, 1985). In intact plants, the water potential of the growing tissue is typically below that of the nearby mature tissue when no transpiration is occurring (Boyer *et al.*, 1985; Cavalieri and Boyer, 1982; Matyssek *et al.*, 1991a). As shown in Fig. 5.4, when the growing tissue is excised, the water potential rapidly decreases by a small amount (Boyer *et al.*, 1985; Matyssek *et al.*, 1991b) because of continued expansion of the walls which decreases (relaxes) turgor after the water and solute flows are disrupted (Boyer *et al.*, 1985; Cosgrove, 1985, 1987; Cosgrove *et al.*, 1984; Matyssek *et al.*, 1988).

The relaxation can be observed over a range of temperatures and is similar as long as some growth is occurring (Fig. 5.4). However,

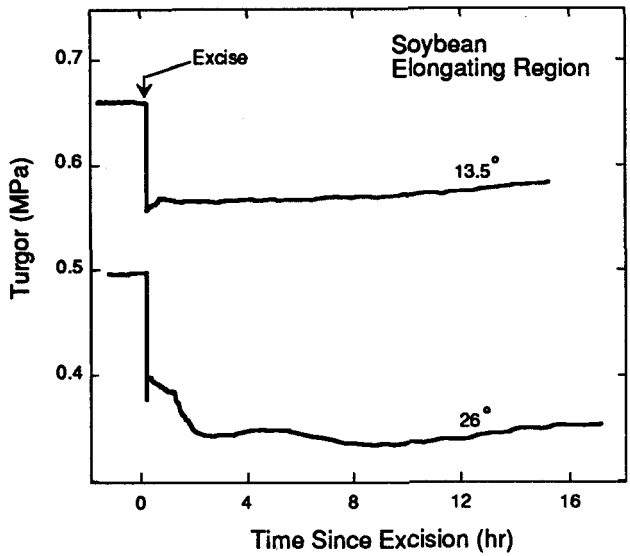

Figure 5.4. Turgor decreases when the stem growing region is excised at temperatures favoring rapid growth (26°C) or slow growth (13.5°C) in soybean seedlings. Turgor initially was measured in an isopiestic thermocouple psychrometer for intact seedlings, and excision occurred at the arrow without disturbing the sample being measured. The stems were growing at the time of excision. Because the excision prevented all water from entering the enlarging cells, the turgor dropped rapidly (5 min) as the walls relaxed after the excision until a threshold turgor was reached below which no further relaxation occurred. Note that the rapid relaxation was similar at the differing temperatures but the growth rate at 13.5°C was only about 5 to 10% of that at 26°C. From Boyer (1993).

the relaxation causes turgor to decrease only about 0.1 MPa (Fig. 5.4) and thus relaxation often cannot be seen within the natural variation between samples. Nonami and Boyer (1989) compared four methods of measuring turgor in soybean stems known to show the relaxation behavior of Fig. 5.4. The data for intact plants in the psychrometer (Fig. 5.5A) did not differ significantly from the data in the excised tissue psychrometer (Fig. 5.5B), the pressure chamber (which also requires excised tissue, Fig. 5.5C), or the miniature pressure probe, which had to penetrate individual cells (Fig. 5.5D). Thus, in many studies, wall relaxation does not significantly affect the measurements.

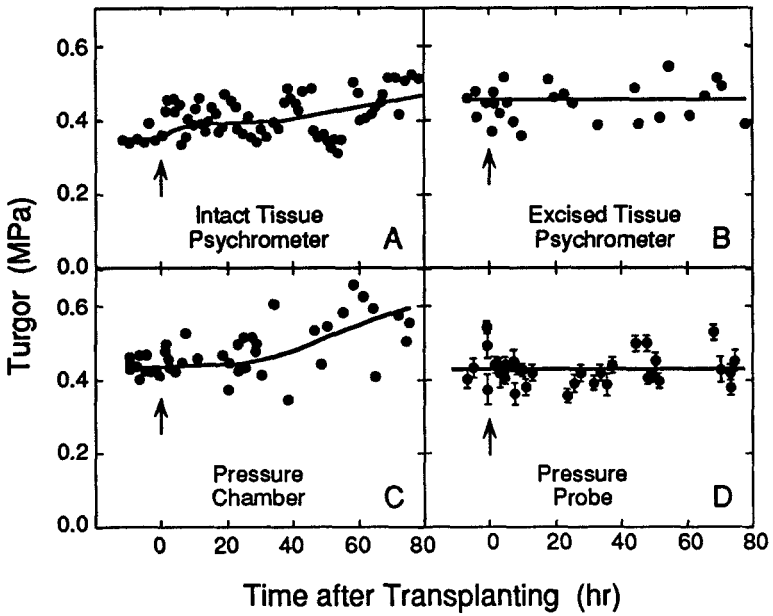

Figure 5.5. Turgor measured by four different methods in growing tissues of soybean stems before and after transplanting to vermiculite having a low water content. The vermiculite water potential at high water content was -0.01 MPa, and at low water content was -0.3 MPa measured with an isopiestic thermocouple psychrometer. Transplanting occurred at the arrow and inhibited growth to near zero within 2 hr. A) Isopiestic psychrometer for intact plants. B) Isopiestic psychrometer for excised tissue. C) Pressure chamber which required excised tissue. D) Miniature pressure probe which penetrated individual cells of intact plants. The turgor for methods A, B and C was measured from the difference between the water potential and osmotic potential. The turgor for method D was measured directly. Data from Nonami and Boyer (1989).

The relaxation sometimes is not seen (e.g., Westgate and Boyer, 1984), usually because it can be delayed for hours if mature or slowly growing tissue is excised with the growing tissue (Boyer *et al.*, 1985; Matyssek *et al.*, 1988). This is because the attached mature tissue acts as a water source that prevents relaxation until the source is depleted (Matyssek *et al.*, 1988, 1991a,b). Previous claims (Cosgrove, 1985; 1987;

Cosgrove *et al.*, 1984) that wall relaxations were large were artifacts caused by these delays followed by large turgor changes (Matyssek *et al.*, 1988).

These experiments indicate that growth can affect measurements of plant water status but, as long as care is taken to ensure that the measurements are stable and made rapidly, they reflect either a small relaxation or no relaxation. Either case is acceptable in practical terms because the effects are generally smaller than the inherent biological variability between samples. For detailed studies of the mechanism of growth, however, knowing the extent of wall relaxation has proven valuable (Kramer and Boyer, 1995).

Growth-Induced Water Potentials

The lower water potential in growing tissue than in mature tissue is growth-induced because it disappears when growth is inhibited by low temperature (Boyer, 1993) or by auxin depletion (Maruyama and Boyer, 1994). Figure 5.6 shows that, in rapidly growing stem internodes of maize, growth was rapid at the base of the internode but not at the top, and the water potential was significantly lower in the base than at the top. This growth-induced water potential did not appear in internodes that were uniformly mature (Fig. 5.6). The measurements were made at the end of the night period when transpiration was negligible and water transport was for growth alone. Similar growth-induced water potentials could be seen in all the growing tissues of the plant (Westgate and Boyer, 1984, 1985) as long as transpiration was minimal.

Plants such as maize are favorable for these kinds of studies because, with the exception of some of the reproductive tissues, all the growing regions are enclosed by other tissues or by soil, and transpiration does not occur directly from the growing tissues. Suppressing transpiration for the whole plant allows the xylem to be at a uniform water potential so that surrounding mature tissues can be compared with growing tissues.

Just as observed with the water potential, the turgor was lower in the growing tissue than in the mature tissue (Fig. 5.6). This indicates that some factor prevented turgor from becoming as high as in nongrowing cells. It appears that the enlargement of the cell wall is

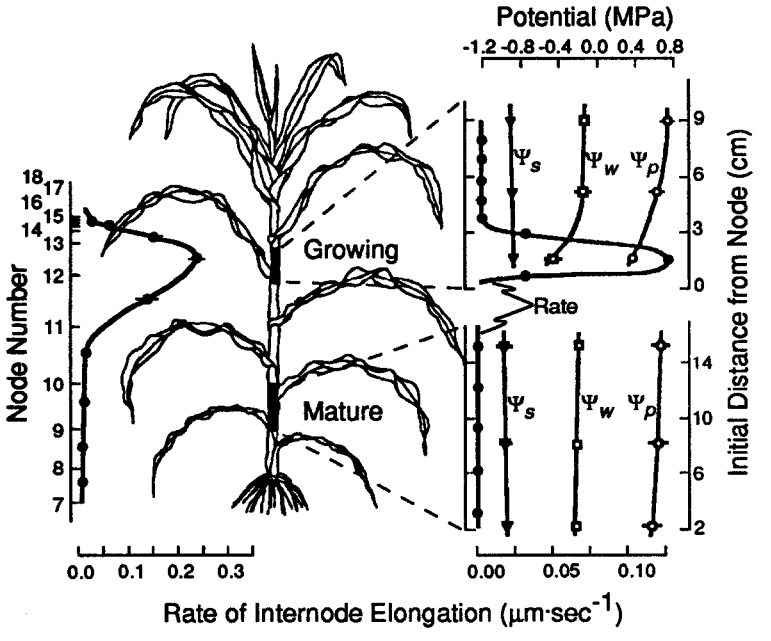

Figure 5.6. The growth and water status of maize stems in predawn conditions when transpiration was negligible. (Left) The distribution of growth along the stem. (Right upper) The distribution of growth within a rapidly growing internode in the upper stem and the water potential (Ψ_w), osmotic potential (Ψ_s), and turgor (Ψ_p) at various positions. (Right lower) As in the right upper graph but for a nongrowing internode at the stem base. The water status was measured with an isopiestic psychrometer using excised tissues. The soil Ψ_w also was measured and was about -0.04 MPa. The mature tissues had a Ψ_w close to that in the soil indicating that the xylem also had a similar water potential. Therefore, the low Ψ_w and Ψ_p of the growing tissues in the upper right graph occurred outside of the xylem in the growing cells. Data from Westgate and Boyer (1984).

rapid enough to prevent a complete buildup of turgor (Boyer, 1968, 1993; Nonami and Boyer, 1987; Maruyama and Boyer, 1994), and the water potential is lowered and transmitted to the apoplast as a tension measurable with the pressure chamber (Nonami and Boyer, 1987). The tension pulls water into the enlarging cells from the xylem. The tension

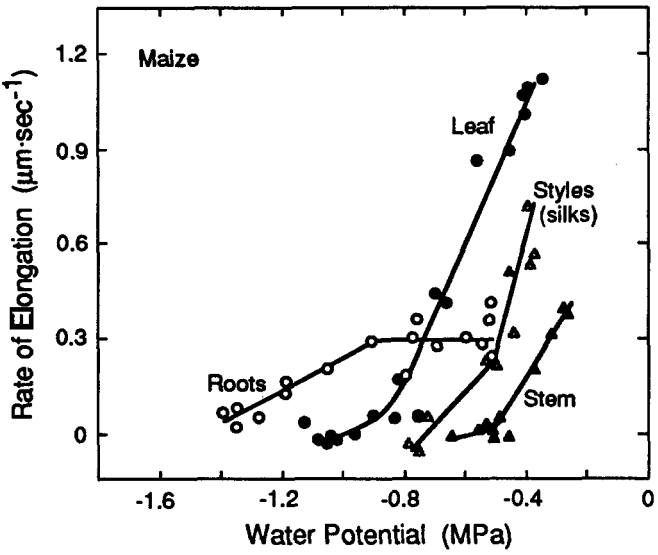

Figure 5.7. Growth of leaf, root, stem, and styles (silks) of maize at various water potentials in the growing region of each organ. Plants were grown in soil from which water was withheld. Water potentials were measured in excised tissue with an isopiestic thermocouple psychrometer at the end of the 10 hr night period when transpiration was negligible. Growth was measured during the entire preceding 10 hr. Data from Westgate and Boyer (1985).

increases until water moves into the cells at a rate that satisfies the demand of enlargement.

Growth at Low Water Potentials

As water potentials decrease, the growth rate often slows. Figure 5.7 shows that maize leaves grew less when water was withheld from the soil sufficiently to decrease the water potential of the growing region at the leaf base (Westgate and Boyer, 1985). The roots of the same plants showed little response until water potentials became very low at the growing root tips. This differential response kept the roots growing while retarding the growth of the leaves and had obvious advantages for a plant coping with dehydrating soil. The growth of the styles (silks) and stem was even more inhibited than in leaves. As the

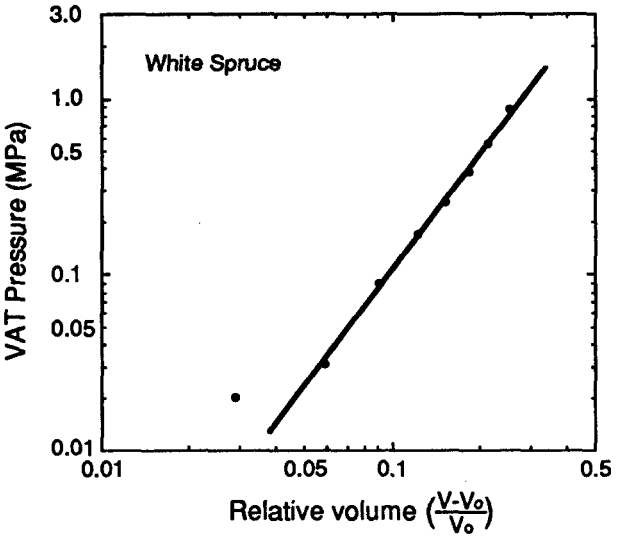

Figure 5.8. Volume-averaged turgor (VAT) at various tissue water contents measured with a pressure chamber in white spruce twigs. The tissue water content is expressed as the amount of water volume V that exceeds the volume at incipient plasmolysis V_o (zero turgor) as a fraction of V_o. Data from Tyree and Hammel (1972).

enlargement of the silks and stem is necessary for flowering in maize, reproductive development was severely retarded by water deprivation. The cause of this differential response is not fully understood but is clearly regulated internally because the water potential was measured in the growing part of each organ, and differences at a given water potential can only be explained by factors within the plant.

Turgor Measured with a Pressure Chamber

When Tyree and Hammel (1972) first showed that the pressure chamber measured the volume-averaged turgor (VAT) in plant tissue, they could easily measure the turgor over the whole range of tissue water contents with a single sample. They observed that a plot of the logarithm of the turgor versus the logarithm of the sample water content (volume) gave a linear relation (Fig. 5.8 shown for white

spruce). Although this is an empirical relationship whose mechanism remains unknown, the linearity held for all the species in the experiment, and the slopes of the lines while different were not widely different. As expected, the line for each species was displaced relative to the others reflecting the difference in water content at which the tissue attained a particular turgor because of the differences in the cell wall elasticity among various species. However, the linearity of the relationship suggests that almost any turgor can be predicted for any water content if the turgor is known at only two points.

Varietal Differences in Midday Water Potential under Field Conditions

Each day, plants undergo changes in water status that reflect the forces required to extract water from the soil. Depending on the frictional resistance of the water path between the leaves and the soil, the water potential of the leaves will need to be higher or lower. Agricultural crops yield best when the water potentials do not become too low during midday because maximum photosynthesis occurs at that time and low water potentials can mean losses in photosynthesis and growth. To prevent leaf water potentials from decreasing to inhibitory levels, root and vascular development must be sufficient to keep the frictional resistance at a moderate level and supply adequate water to the leaves. However, too much root and vascular tissue can be deleterious because it uses dry matter that otherwise could be devoted to marketable yield. Therefore, geneticists and breeders fit plants genetically to the water demand of the region where the plants will be grown. This is usually done with yield trials that integrate all the yield factors in a particular region, automatically selecting for optimum frictional resistance for water flow.

We can see how this occurs by comparing the midday leaf water potentials of older cultivars with those of newer cultivars of soybean when the plants are grown together in the same field (Boyer *et al.*, 1980). Because the cultivars have a common water source, differences in leaf water potential indicate differences in frictional resistances among the cultivars. Figure 5.9 shows that Wayne, a newer cultivar, had a leaf water potential close to -1.2 MPa in midday but the other cultivars had lower water potentials measured in the field with

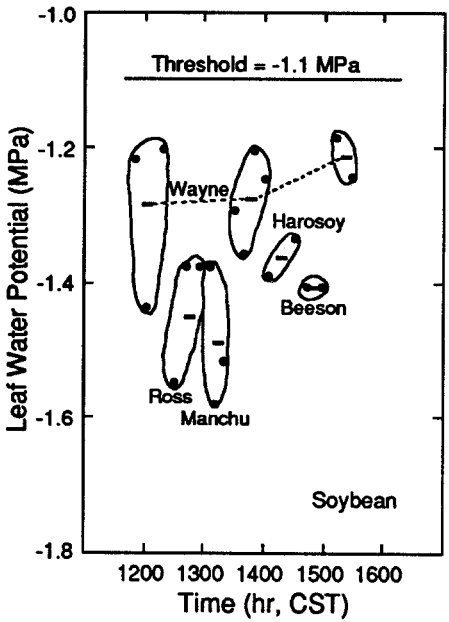

Figure 5.9. Leaf water potential measured with a pressure chamber during the afternoon in various cultivars of soybean growing in the same field in Urbana, Illinois. Closed circles are individual measurements and the bars are the means for each cluster of measurements. The measurements were made only in (1) fully exposed leaves perpendicular to the incoming radiation, (2) at the top of the canopy, (3) when reference water potentials (in Wayne) were stable, and (4) in a portable pressure chamber standing next to the plant to ensure minimal water loss after excising the leaf. The threshold water potential of -1.1 MPa indicates the potential below which photosynthesis is inhibited. Data from Boyer *et al.* (1980).

a pressure chamber. In soybean, photosynthesis is inhibited when leaf water potentials are below -1.1 MPa (Boyer, 1970; Ghorashy *et al.*, 1971; Huang *et al.*, 1975), and the water potentials exhibited by the various cultivars could inhibit photosynthesis as much as 50%.

Figure 5.10 shows that, among soybean cultivars in Maturity Group II where Beeson is the newest cultivar (introduced in 1968) and the older cultivars are part of the Beeson lineage, the yield increased as newer cultivars were released by plant breeders but the midday water

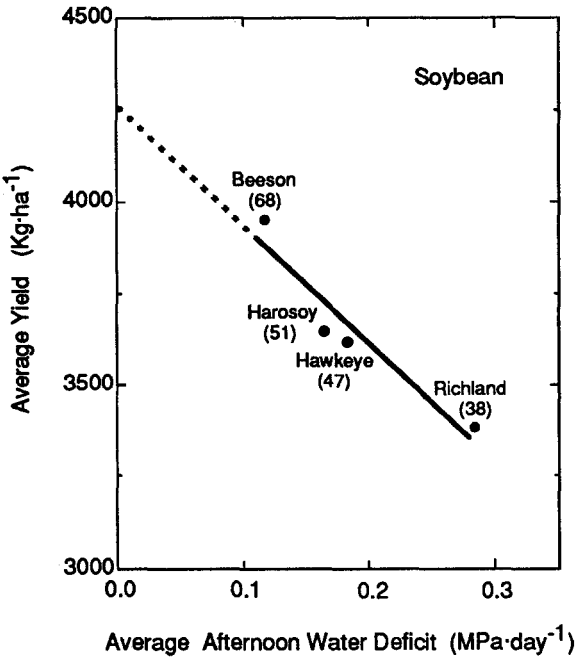

Figure 5.10. Average yields over three growing seasons and average afternoon water deficits in older and newer soybean cultivars measured in the field with a pressure chamber in Urbana, Illinois. The date of release of the cultivars is shown in parentheses. Older cultivars were part of the genetic lineage for the newest cultivar (Beeson). Water deficits were calculated as the average water potential below the threshold of -1.1 MPa each day. Extrapolating the dashed line to the Y-axis shows the yield increase expected if afternoon water deficits are eliminated. Water potentials were measured with a pressure chamber. Data from Boyer *et al.* (1980).

potential also increased. Thus, plant breeders were improving water transport while they improved yield. From such a plot, it can be predicted that the yield of Beeson can be improved another 9% if selections could bring midday water potentials to -1.1 MPa (extrapolation shown in Fig. 5.10). This process could be accelerated by measuring midday water potentials directly and selecting elite lines that have water potentials in the desired range.

There are certain measurement principles that need to be followed for successful cultivar comparisons in the field using a pressure chamber or psychrometer. First, careful attention is paid to keeping variation to a minimum. The main interest is in the midday water potential when photosynthesis is most rapid, and leaves are selected that are fully exposed to the sun and perpendicular to the incoming radiation. Second, the leaves are in the upper part of the canopy. This ensures that the flow path from the soil to the leaf is about the same length. Leaves lower in the canopy display water potentials that are less negative than in the upper canopy. Third, the comparisons are made during a part of the day when water potentials are stable. In the example of Fig. 5.9, this was done by repeatedly measuring a reference cultivar (Wayne) to evaluate the stability of the water potential. Comparisons were made between cultivars only during the stable time. Fourth, the pressure chamber is mounted on a portable cart and taken directly to the plant to be sampled or the psychrometer is taken to the field and loaded at the plant. This keeps sampling time to 10 sec or less and ensures that the water potential of the leaves is as reproducible as possible. Leaves should not be stored for later measurement.

Such precautions become essential because field comparisons are made in a variable environment that can cause the data to have too much scatter. The cultivar differences in Fig. 5.9 were about 0.2 MPa at the extreme and one would like to reliably detect even smaller differences. In the water potential range for soybean, small differences have a large effect on photosynthesis because the responsiveness of photosynthesis is so large (Boyer *et al.*, 1980).

Osmotic Adjustment

While comparing the water potential and osmotic potential of soybean seedlings, R.F. Meyer discovered that they adjusted osmotically when the root medium dehydrated (Meyer and Boyer, 1972). The adjustment was caused by an accumulation of solutes. As a result, the turgor scarcely changed. The maintenance of turgor implied that the water content of the tissue also remained high and this ultimately was shown to be the case (Bozarth *et al.*, 1987), indicating that the adjustment allowed more water extraction from the soil than otherwise would occur.

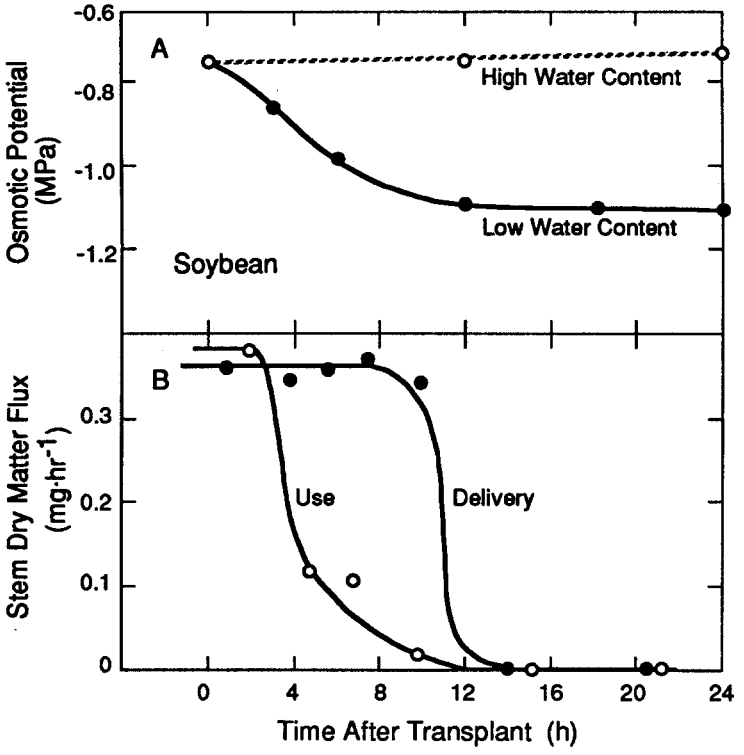

Figure 5.11. Osmotic adjustment and dry matter fluxes in the growing region of soybean stems after transplanting the seedlings to vermiculite of low water potential (Low Water Content) or high water potential (High Water Content). The decrease in osmotic potential (A) was caused by continued solute delivery to the growing cells but slower use (B). The osmotic potential became more negative when delivery exceeded use. Growth decreased in the first 2 hr after transplanting. The osmotic potential was measured with an isopiestic thermocouple psychrometer. Data from Meyer and Boyer (1981).

The solutes were mostly sugars and amino acids, and because dehydration did not occur in the tissues and the number of cells did not change in the growing region, there was an absolute increase in the number of moles of solute per cell (Meyer and Boyer, 1972). Figure 5.11A shows the decrease in osmotic potential as the root medium dehydrated, and Fig. 5.11B shows that solute delivery to the growing cells remained high but solute use declined (Meyer and Boyer, 1981).

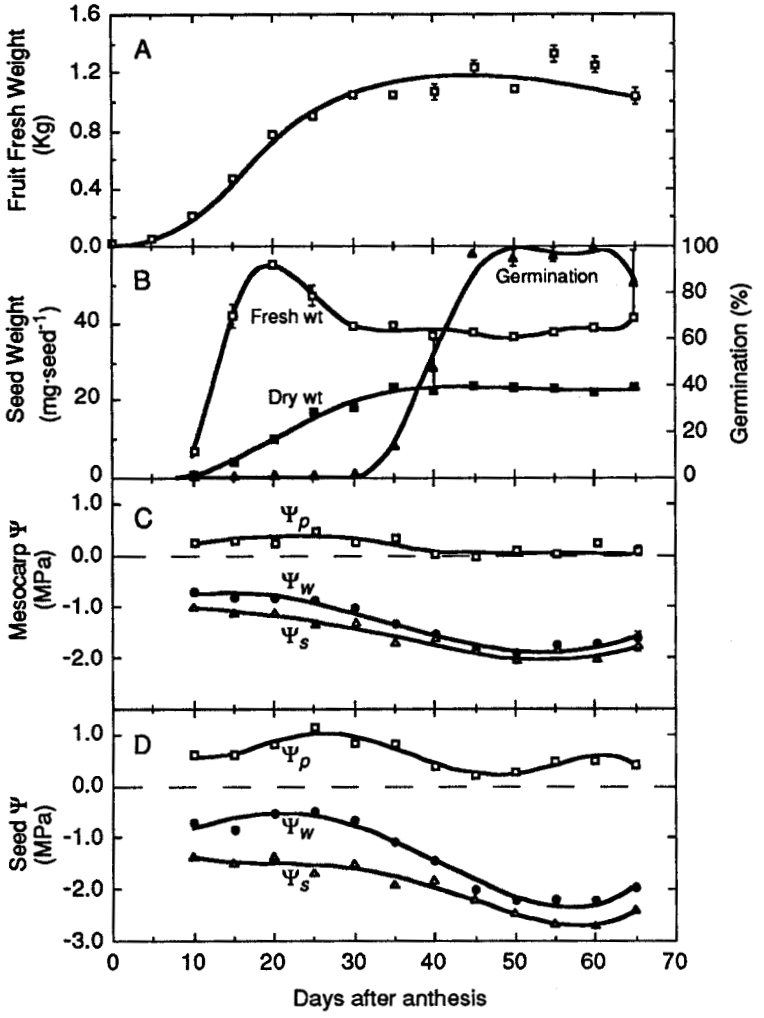

Figure 5.12. Development and water status at various times in muskmelon fruit and seed measured with a calibrated dew point hygrometer. A) Fruit fresh weight, B) seed fresh weight, dry weight, and germinability, C) water potential (Ψ_w), osmotic potential (Ψ_s), and turgor (Ψ_p) of the mesocarp of the fruit wall, and D) Ψ_w, Ψ_s, and Ψ_p of the seeds. Note the parallelism in Ψ_w, Ψ_s and Ψ_p between C and D. Data from Welbaum and Bradford (1988).

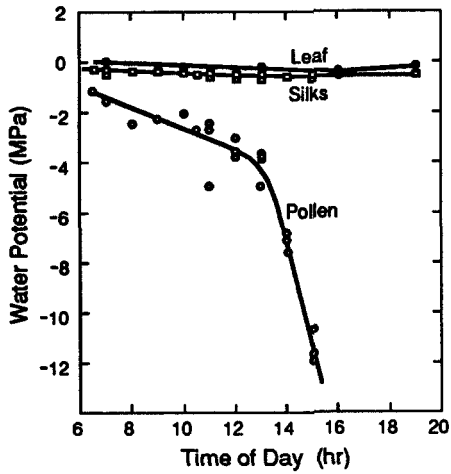

Figure 5.13. Water potentials of pollen, styles (silks), and leaves measured with an isopiestic thermocouple psychrometer in the same maize plants growing under field conditions in Urbana, Illinois. The pollen was freshly collected from anthers that had dehisced at dawn the same day. The silks were growing but were covered and had not been exposed to pollen. The leaves were sampled at the leaf tip which was mature. The psychrometers were rapidly loaded with samples in the field and transported back to the laboratory. Data from Westgate and Boyer (1986).

The high rate of delivery but low rate of use caused solute to accumulate in the cells resulting in the osmotic adjustment. After 15 to 20 hr, delivery also declined and came into balance with use (Fig. 5.11B). The balance caused the osmotic potential to stabilize, and no further changes occurred. Osmotic adjustment is thus driven by decreased solute use rather than increased transport or accelerated rates of hydrolysis.

Water Relations of Reproductive Tissues

The reproductive structures of plants develop rapidly and often require large amounts of water and solute. Welbaum and Bradford (1988) found that muskmelon fruits required about 30 days to enlarge during which the fresh weight gained over 1 kg most of which was

water. The seeds enlarged early and laid down dry weight later (Fig. 5.12B), and throughout development the water potential of the mesocarp (fleshy wall of the fruit) and of the seeds was significantly below zero, suggesting that water potential gradients were present and favored water movement into the fruit (Figs. 5.12C and 5.12D). The water potential of the seeds decreased to -2.0 MPa at maturity (about 50 days) despite never having been exposed to a dehydrating atmosphere. The dehydration of the seed probably was caused by the low osmotic potentials surrounding the seeds (Figs. 5.12C and 5.12D).

Related work explored the water status of maize flowers and showed that the water potential of pollen was about -2.0 MPa at sunrise and -11 MPa by midafternoon (Westgate and Boyer, 1986), which was much lower than in growing styles (silks) or leaves (Fig. 5.13). This extreme desiccation occurred inside the locules of anthers that had dehisced at sunrise and illustrates that pollen desiccation is rapid even in that protected environment. The pollen was viable at the lowest water potential and able to fertilize the ovules. The low water potential allowed water to be absorbed from the surrounding stylar tissue and probably was essential for pollen tube growth. The styles were in contact with the water supply in the xylem and thus were able to supply water to the pollen tube.