Plant Physiol. (1989) 89, 798-804
0032-0889/89/89/0798/07/$01.00/0

Received for publication April 7, 1988
and in revised form September 16, 1988

Turgor and Growth at Low Water Potentials[1]

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ABSTRACT

Turgor affects cell enlargement but has not been measured in enlarging tissue of intact plants when growth is inhibited by inadequate water. Mature or excised tissue can be problematic for these measurements because turgor may not be the same as in intact enlarging cells. Therefore, we measured the average turgor in the elongating region of intact stems of soybean (*Glycine max* [L.] Merr.) while the seedlings were exposed to low water potentials by transplanting to vermiculite of low water content. Stem growth was completely inhibited by the transplanting, and the average turgor decreased in the mature stem tissue. However, it did not decrease in the elongating region whether measured in intact or excised tissue (total of four methods). At the cellular level, turgor was uniform in the elongating tissue except at transplanting, when turgor decreased in a small number of cortical cells near the xylem. The reduced turgor in these cells, but constant turgor in most of the cells, confirmed that no general turgor loss had occurred but indicated that gradients in water potential extending from the xylem into the enlarging tissue were reduced, thus decreasing the movement of water into the tissue for cell enlargement. A modest growth recovery occurred after 2 days and was preceded by a recovery of the gradient. This suggests that under these conditions, growth initially was inhibited not by turgor loss but by a collapse of the water potential gradient necessary for the growth process.

Plants grow in size mostly by increasing in cell water content. The enlargement occurs because solute concentrations are high enough inside the cells to extract water osmotically from the surroundings. As a result, the pressure in the cells (turgor) rises and extends the walls irreversibly, enlarging the cell compartment.

The dependency of these processes on water causes growth to respond to the supply of water in the soil. Effects are particularly apparent for organs in the shoot, which may be inhibited during vegetative or reproductive development (33) with large consequences for plants.

The depletion of soil water decreases water potentials (Ψ_w) in the plant and also can decrease the turgor. Effects on growth often are attributed to this turgor loss (2, 16). However, the discovery that plants adjust osmotically to low Ψ_w (14, 23) was followed by reports that turgor was maintained, sometimes completely, while growth was inhibited (12, 13, 20, 21, 24, 25, 33). If turgor does not fall, the growth inhibition must be attributed to other factors. Several possibilities have been suggested (3, 7, 20, 32) but doubt exists because the turgor measurements (12, 13, 20, 21, 24, 25, 33) involved excised tissue, sometimes from nongrowing parts of the plant. Turgor was observed to change after excision (3, 11), and was not the same in growing and nongrowing tissues (25).

Except for a preliminary report (17), turgor measurements are not available for intact plants whose growth was affected by low Ψ_w. Therefore, we investigated turgor in elongating tissues under these conditions. We used stems of dark-grown soybean seedlings because the turgor could be measured by several methods in the large and exposed growing region. By conducting the experiments in the dark in a saturated atmosphere, transpiration was avoided and turgor reflected only the processes affecting growth.

MATERIALS AND METHODS

Plant Material

Soybean (*Glycine max* [L.] Merr. cv Wayne) seeds were disinfected in a 1% solution of NaOCl for 5 min, rinsed with flowing water for 1 h, sown in vermiculite with adequate water (5.0 mL of 0.1 mM $CaCl_2$/g of vermiculite, *i.e.* Ψ_w = −0.01 MPa measured psychrometerically as described below), and grown at 29 ± 0.5°C and saturating humidity in darkness. After 55 to 60 h, they were transplanted to a 200 mL beaker containing either similar vermiculite (1× treatment) or water-deficient vermiculite (⅛ the amount of water = ⅛× treatment = 0.63 mL of 0.1 mM $CaCl_2$/g of vermiculite, *i.e.* Ψ_w = −0.28 ± 0.02 MPa measured psychrometrically). The vermiculite and $CaCl_2$ solution were shaken together prior to transplanting to ensure uniform mixing. After transplanting, the seedlings were returned to the growth environment. All seedling manipulations were done under a green safelight (green fluorescent bulb wrapped in green plastic sheet having maximum transmission at 525 nm and negligible transmission below 475 nm and above 575 nm).

Measurement of Growth

Stem (hypocotyl) length was measured with a ruler at intervals of 5 to 13 h in 8 plants for each measurement. Detailed measurements of growth rate were obtained with a radial displacement transducer clamped to the upper part of the stem. The clamp was counterbalanced to be weightless. A rigid reference bar was clamped to the lower stem. The length between the transducer and rigid bar was recorded electrically. Growth rate was measured from the changing stem length as a function of time. The transducer and bar were mounted on a microscope, the fine adjustment of which could be used to calibrate the instrument without disturbing the seedling.

Measurement of Water Status

The turgor of the stem tissue was measured by four different methods that gave average values for the region measured.

[1] Support for this work was provided by United States Department of Energy grant No. DE-FG05-84ER13273.

The first used the isopiestic technique with a thermocouple psychrometer for excised tissue (4) to allow comparison with past measurements (6, 8, 20, 23, 25, 33). Four tissue samples 1.5 cm long were excised from the stem region between 0.5 and 2.0 cm behind the cotyledons in the zone of elongation (most rapidly growing part, see 3, 8, 22, 23 for exact location of elongating region at various ages). These were placed on the bottom of a psychrometer chamber that had been coated with melted and resolidified petrolatum. After measuring Ψ_w, the osmotic potential Ψ_s was determined in the same tissue immediately after freezing at −70°C and thawing. The turgor was calculated by subtracting Ψ_s from Ψ_w. No correction was made for dilution by the cell wall solution (5) because the wall occupied only 3.9% of the total cell volume (26). Vermiculite was measured as with the tissue, except a sample of vermiculite was placed on the bottom of the psychrometer chamber and was Ψ_s not determined.

The second method used an isopiestic psychrometer for intact seedlings (guillotine psychrometer [3]). Four stems of intact seedlings were sealed into a thermally stable chamber inside of which was a small vapor pressure chamber for a thermocouple. The roots were outside the apparatus and extended into 1× vermiculite. The vapor pressure chamber was coated with petrolatum and the same material was used to seal the four stems into the chamber so that 1.5 cm of the elongating region was inside. The low friction of the petrolatum allowed the plants to grow during the measurement. A thermocouple bearing a sucrose solution of known Ψ_w was placed in the vapor pressure chamber to measure tissue Ψ_w. Wherever possible, the measurement was isopiestic, *i.e.* the vapor pressure of the solution was the same as that of the tissue and no net vapor exchange took place. This prevented errors caused by the diffusive resistance of the tissue to water vapor transfer and assured that the tissue neither hydrated nor dehydrated during the course of the measurement (4). After a period of growth, the seedlings were transplanted by removing the 1× vermiculite and adding ⅛× vermiculite around the root system. Because humidities were saturating, the water content of the vermiculite was constant for the duration of the experiment.

The Ψ_s was measured in similar seedlings grown at the same time. The elongating stem tissue was excised, the segments were placed in a hypodermic syringe, frozen, thawed, and pressed to release the cell solution. The solution was placed on a thermocouple junction and its Ψ_s was measured by isopiestic technique. Tissue turgor was calculated by subtracting Ψ_s from Ψ_w. For reasons stated above, no correction was made for dilution by the cell wall solution.

The third method of measuring the turgor used a pressure chamber (1, 30). An intact seedling was placed into the chamber so that the zone of elongation of the stem (about 1.5 cm) was inside and the nonelongating ('mature') part of the stem (about 3 cm) was sealed in the lid and extended to the outside. Just above the lid, the stem and roots were excised with a razor blade. The presence of the mature tissue delayed changes in turgor after the excision, thus keeping turgor at the level in the intact plant during the measurement (3, 22, 28). The humidity was kept at saturation inside and outside of the chamber to prevent evaporation from the seedling surfaces. For some measurements, the exudate from the cells injured during excision was allowed to be reabsorbed by the growing stem before pressurizing the tissue. For other measurements, this process was shortened by removing the exudates with a filter paper before pressurization. There was no difference in the results by the two methods (28). The seal was gently tightened until no gas leakage occurred. Pressure was then applied to hold xylem exudates at the level of the cut surface of the stem. Because the xylem solution was dilute (about −0.04 MPa), the balancing pressure was considered to be the Ψ_w of the elongating region (1, 28). After determining the Ψ_w, the elongating region was immediately placed in a hypodermic syringe and Ψ_s was measured as described for the psychrometer measurements for intact seedlings. Tissue turgor was calculated by subtracting Ψ_s from Ψ_w.

The fourth method used the miniature pressure probe (18) to measure turgor directly in the cells of the stems of the intact seedlings. To protect the seedlings from water loss, stems were coated with petrolatum, and the vermiculite surface was covered with plastic film (29). The stem of the seedling also was covered with a wet tissue paper on top of the petrolatum to minimize possible water loss. To use the pressure probe, a small window was cut in the wet tissue paper.

The probe consisted of a microcapillary connected to a small chamber containing a pressure transducer. The entire instrument was filled with silicon oil. When the microcapillary tip was introduced into a cell, the turgor pushed the oil back into the capillary, leaving a meniscus at the cell solution/oil boundary in the tip. The position of the meniscus could be seen through a microscope and could be changed by moving a metal rod into the chamber to displace the oil. The position of the meniscus was controlled manually using the controls for an adjustment motor for the rod. The turgor was read directly from the transducer output when the meniscus was returned to the position it occupied before insertion of the tip into the cell. Care was taken to test each measurement for leaks according to the procedures of Nonami *et al.* (29).

The turgor was measured in cells of the cortical tissue. The length and width of the cells were 300 to 370 μm and 55 to 70 μm, respectively. The volume was 700 to 1450 pL, about 80% of which was vacuole. The diameter of the capillary tip was about 2 to 4 μm and, when inserted 20 to 40 μm inside a cell, the volume of glass introduced into the cell was estimated to be 0.4 to 1.7 pL. To demonstrate hydraulic continuity between the interior of the probe and the cell solution, small volumes of solution (5–10 pL) were moved in and out of the probe repeatedly (29). To measure the average turgor of a tissue region, turgor was measured in 12 to 71 cells and averaged.

RESULTS

The elongation of the stems was rapid when water was available but was inhibited when the plants were transplanted to ⅛× vermiculite (Fig. 1A). The inhibition began immediately and was most severe 10 to 40 h after transplanting (Fig. 1B). At this time, rates approached zero. Thereafter, elongation began to recover and eventually reached 60% of the control rate (Fig. 1B). The control plants (1×) grew rapidly with scarcely any hesitation attributable to transplanting (Fig. 1).

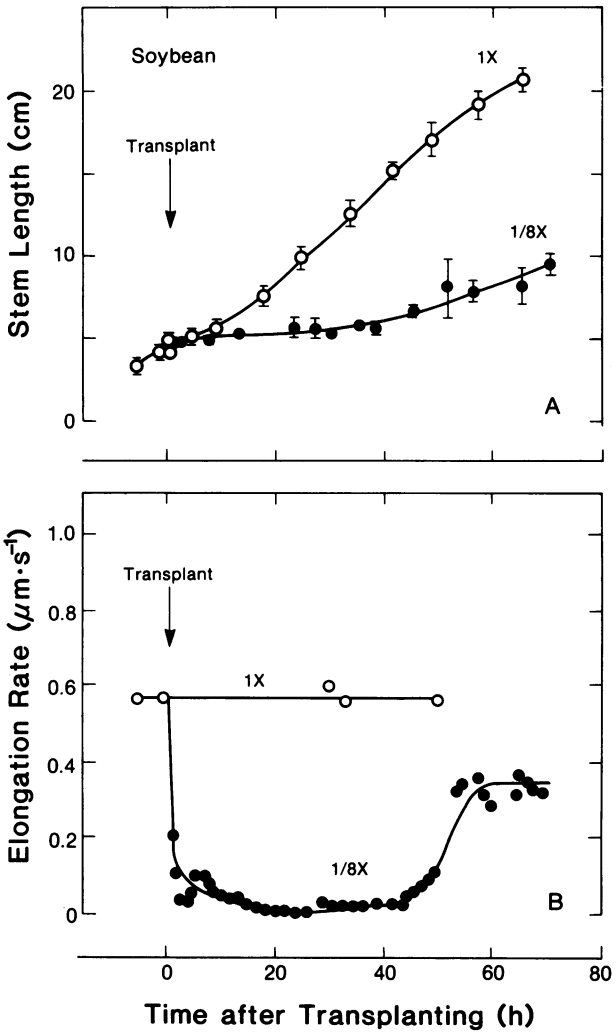

Figure 1. Stem length (A) and growth rate (B) of stems of soybean plants grown in the dark in the presence of adequate water (1×) or low amounts of water (⅛×) in vermiculite. The seedlings were transplanted to the vermiculite at the arrow. Vertical bars indicate 95% confidence intervals (Student's *t* distribution).

The thermocouple for excised tissue indicated that the vermiculite Ψ_w (−0.01 MPa) was initially higher than in the elongating tissue (−0.3 MPa). This favored water uptake by the tissue (Fig. 2A). After transplanting, the vermiculite Ψ_w decreased to the tissue Ψ_w and collapsed the Ψ_w difference favoring uptake. Subsequently, the tissue Ψ_w decreased slowly, reestablishing the Ψ_w difference. This reestablishment preceded the recovery in growth (*cf.* Figs. 1 and 2A). The Ψ_s decreased slowly by about the same amount as the Ψ_w. The turgor (calculated by difference) was about 0.45 MPa initially and constant throughout the experiment (Fig. 2B). Turgor also was constant in the controls (data not shown).

These results were compared with those obtained in a thermocouple psychrometer for intact plants (guillotine psychrometer [3]). As with the excised tissue, the Ψ_w of the vermiculite was higher than in the intact elongating tissue before transplanting (Fig. 2C). Upon transplanting, this difference decreased to zero. The Ψ_w of the tissue then decreased slowly to about 0.7 MPa and was paralleled by a decrease in Ψ_s. Turgor initially was about 0.35 MPa and remained stable after transplanting. By the end of the experiment, it appeared to increase slightly (Fig. 2D). It is important to note that this method permitted a continuous recording of Ψ_w and any rapid change in turgor would have been detected as a rapid change in Ψ_w. Also, because the plants were completely intact and Ψ_w was measured remotely while growth responded to low Ψ_w, there could have been no excision or wounding effects.

With the pressure chamber, the Ψ_w and Ψ_s (Fig. 2, E and F) were similar to those measured with the psychrometers (Fig. 2, A–D). Turgor initially was about 0.45 MPa and stable after transplanting (Fig. 2F) but appeared to increase slightly by the end of the experiment.

The turgor measured in the elongating region with the pressure probe was about 0.42 MPa initially (Fig. 3A). It remained constant after transplanting (Fig. 3A), confirming the results from the other methods.

In contrast, the pressure probe detected large turgor transitions in the mature tissue at the base of the same stems. Figure 3B shows that turgor was initially about 0.40 MPa and decreased to 0.1 MPa after transplanting before recovering at 45 h. Because there was negligible transpiration (stems in saturated atmosphere, coated with petrolatum, covered with wet tissue paper), these transitions must have been caused by water moving out of the tissue into the xylem followed by flow in the reverse direction. The measurements in the elongating and mature tissues were made in the cortical cells 100 to 375 μm below the stem surface, a region accounting for 60% of the volume of the stem tissue.

The change in turgor of the mature tissue implies that the xylem Ψ_w was fluctuating. If so, the changes in xylem Ψ_w might have extended into the elongating tissue. We measured turgor in deeper cells around the xylem in the elongating tissue. These cells (Fig. 4, inner cells) initially had a turgor (0.45 MPa) similar to the turgor of the rest of the tissue (Fig. 4, outer cells) but, immediately after transplanting, they lost turgor. The loss coincided with the decreased rate of growth (Fig. 4). Turgor recovered after 12 h. The recovery preceded the recovery in growth. Throughout the experiment, the outer cells of the same plants showed no turgor change, in agreement with the results in Figures 2 and 3. For the inner cells, measurements were 500 to 875 μm below the stem surface (representing about 20% of stem volume). The xylem was about 750 μm below the surface. For the outer cells, measurements were 100 to 375 μm below the surface (60% of stem volume).

DISCUSSION

The data indicate that, although growth was markedly inhibited by low Ψ_w, turgor was not the cause. Turgor would need to decrease throughout the elongating tissue to account for the decrease in growth. This is because, if each cell grows without constraint by the other cells, all the cells would need to change turgor together to maintain coordinated growth. If, on the other hand, growth is constrained by the outer layers of cells (19), turgor would need to change in enough cells to decrease the force on the outer layers. Thus, regardless of how

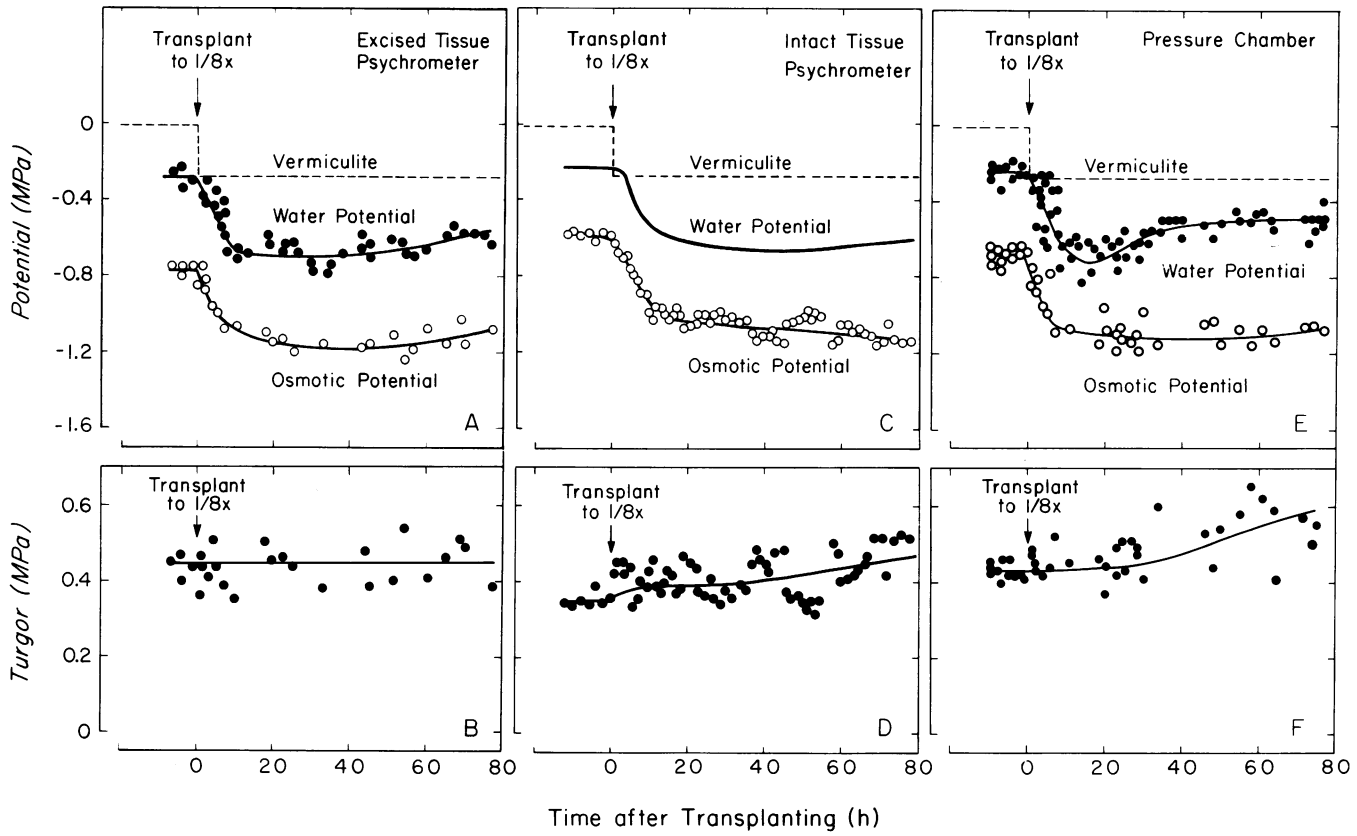

Figure 2. Water potential, osmotic potential, and turgor in the zone of elongation of soybean stems grown as in Figure 1. The measurements were made with an isopiestic psychrometer using excised segments (A and B), a guillotine psychrometer using intact seedlings (C and D), and a pressure chamber using excised stems (E and F). In C and D, growth in the intact seedlings occurred rapidly (0.30–0.45 $\mu m \cdot s^{-1}$) in the psychrometer before transplanting. Water potential data are shown as a continuous recorder tracing in C, otherwise as individual measurements.

growth is organized, a turgor decrease would be detected in the tissue as a whole.

That this did not occur was clear in all four methods used in this study. Contrasting behavior occurred in the mature stem tissue where turgor decreased dramatically, then increased. Because the data were collected in the same plants measured by the same method (pressure probe), turgor loss would have been apparent in the elongating region if it had occurred.

Turgor loss also did not occur transiently in the elongating tissue as a whole. Because the guillotine psychrometer had a rapid response (half-time = 36 s [3]) and measured Ψ_w continuously while the plants were intact and growing, even a very brief turgor transient would have been seen as a Ψ_w transient. Because no transients were detected, the growth inhibition must have been caused by some factor other than a decrease in turgor.

This is in contrast to the results reported by Hsiao and Jing (17) who exposed roots to high, growth-inhibiting concentrations of sorbitol and observed transient losses in root turgor. The high concentrations likely caused a rapid dehydration that is rarely seen in nature, and thus the transient turgor loss normally would not occur. There was also the possibility that sorbitol entered the root, altering the turgor. We used vermiculite of low water content rather than concentrated solutions to avoid this type of dehydration and solute penetration. The vermiculite should have simulated the conditions present during natural water depletion in the soil.

What then caused the inhibition of growth in our experiments? We propose that the change of turgor that occurred in the cells next to the xylem was important. While the turgor change occurred in too few cells to itself be the cause, it indicates that the Ψ_w of these cells must have changed.

The average Ψ_w of the cells in the elongating tissue was about −0.3 MPa before transplanting. In similar seedlings grown identically, we observed a xylem Ψ_w close to zero (3, 6, 8, 26). Thus, during rapid growth, a potential gradient extended radially from the xylem into the elongating tissue. In three dimensions, this formed a potential field around the xylem that provided the force to extract water from the xylem for the growth process (28).

Lowering the xylem Ψ_w by transplanting would reverse the field and reverse the direction of water movement. Water entry into the surrounding tissue would be inhibited, decreasing growth. The key to this concept is that a modest decrease in Ψ_w in the xylem would not affect the bulk Ψ_w of the elongating tissue initially because the bulk Ψ_w already would be low.

Evidence for this effect was observed with each of the techniques we used. The four techniques showed that, before

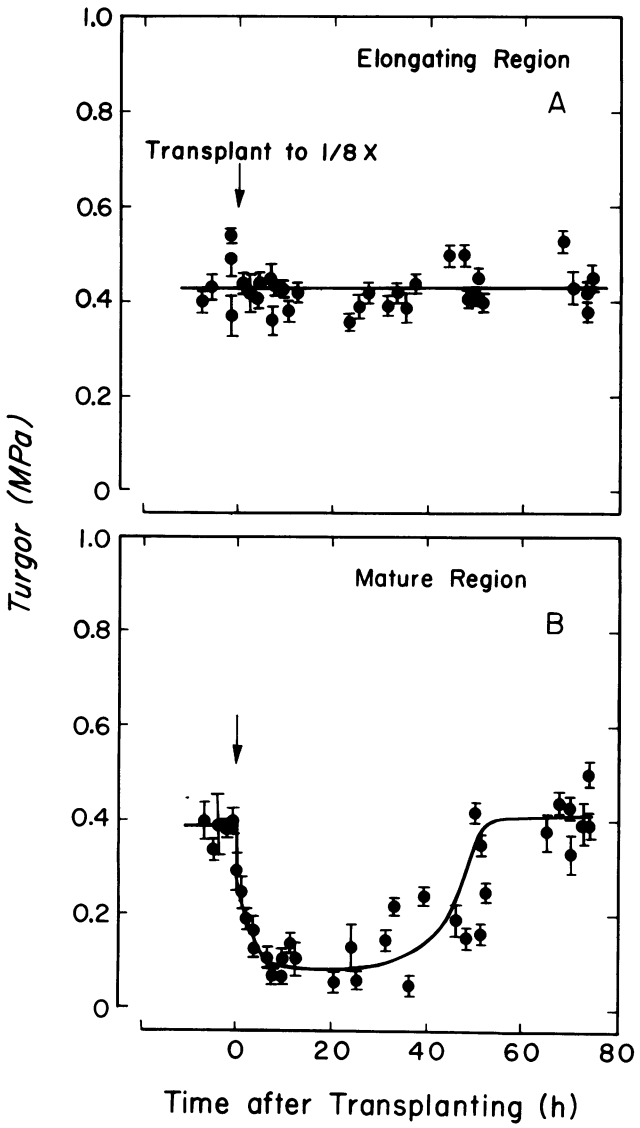

Figure 3. Turgor of the outer cortical cells in the elongating region (A) and basal mature region (B) in the same intact seedlings, grown as in Figure 1 and measured with a pressure probe. Each point is the average turgor of 12 to 71 cells located 100 to 375 μm below the surface of the stem in a single seedling. Vertical bars indicate 95% confidence intervals (Student's t distribution).

transplanting, the Ψ_w of the vermiculite and the mature tissue was higher than that of the elongating tissue, demonstrating the presence of a gradient favoring water movement into the elongating tissue when growth was rapid. At transplanting, the Ψ_w of the vermiculite was lowered to that of the elongating tissue (−0.2 to −0.3 MPa), collapsing the gradient. This effect was confirmed by the decrease in xylem Ψ_w by about the same amount, as shown by the decrease in turgor in the cells near the xylem (decreased about 0.2 MPa) and by the decrease in turgor in the mature tissue (0.2–0.3 MPa), which could only occur if xylem Ψ_w had decreased.

The kinetics of these changes also are consistent with the concept that the inhibition was caused at least initially by an inability of the enlarging cells to extract water from the vascular system. The potential field changed very rapidly (shown by the cells near the xylem) and growth was inhibited simultaneously. The recovery of the potential field preceded the recovery of growth.

The collapse of the potential field that occurred after transplanting is shown diagrammatically in Figure 5. Before transplanting, growth was rapid and Figure 5A indicates that turgor was uniform in the elongating tissue. A Ψ_w field was present that would move water from the xylem into the cells. After transplanting, Figure 5B shows that the Ψ_w decreased in the xylem, reversing the field in nearby cells and inhibiting growth. The turgor decreased soon thereafter in the cells next to the xylem (Fig. 5C). Growth was immediately inhibited (beginning at Fig. 5B) because it depended on water extracted from the xylem where the potential field was in the wrong direction. Note that the Ψ_w and turgor did not change in the outer cells in Figure 5, A to C. With time, however, the change in Ψ_w would be transmitted to the outlying tissues and the Ψ_w would decrease in the tissue as a whole, as was observed after 3 h (Fig. 2).

With extended times beyond 3 h, the Ψ_w gradient was completely reestablished as the Ψ_w decreased in the cells (Fig. 2). The reappearance of the gradient was not caused by decreased turgor, which remained constant during this time. An osmotic adjustment (27) occurred gradually during the 10 to 20 h after transplanting (shown by the decrease in Ψ_s of

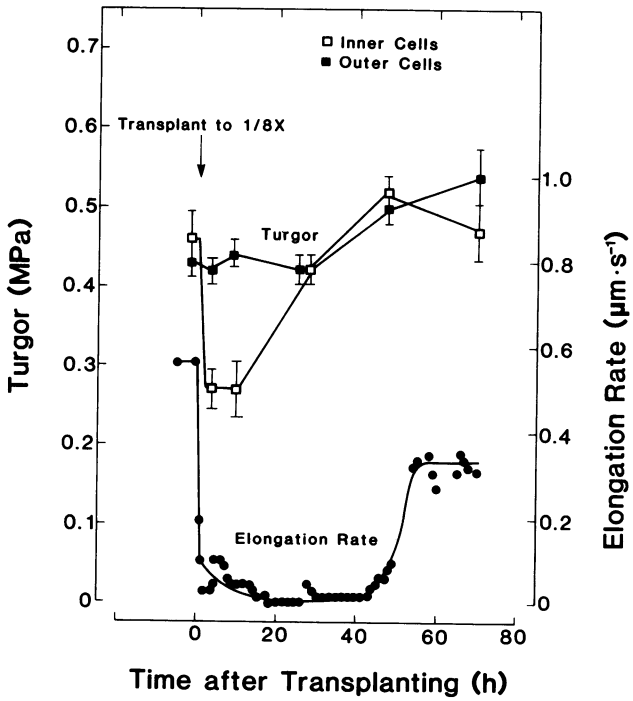

Figure 4. Comparison of average turgor of the inner and outer cortical cells in the elongating tissue in the same intact seedlings, grown as in Figure 1 and measured with a pressure probe. The rate of elongation is also shown from Figure 1 for comparison. The average turgor was obtained from 24 to 38 cells per data point. Outer cells were 100 to 375 μm below the stem surface; inner cells, 500 to 875 μm below the surface. Vertical bars indicate 95% confidence intervals (Student's t distribution).

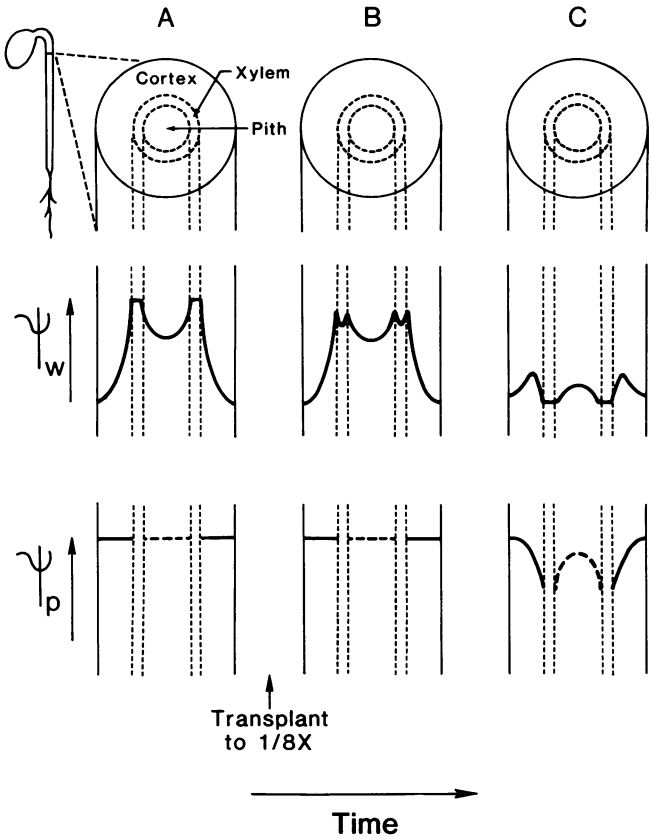

Figure 5. Schematic conception of the water potential (Ψ_w)and turgor (Ψ_p) profiles extending radially from the xylem in the zone of elongation for plants grown as in Figure 1. At (A), rapid growth is occurring immediately before transplanting. At (B), growth is inhibited during the first h after transplanting. At (C), growth continues to be inhibited about 3 h after transplanting. Based on Molz and Boyer (26) and the data in Figs. 1, 2, and 4 for intact seedlings.

the elongating tissues), and this served to maintain turgor. Cell hydration was constant (7) indicating that the osmotic adjustment was caused by an accumulation of solute rather than a loss of water by the cells. Cotyledonary reserves were the source of the solute (24). Thus, over these longer times, growth was not inhibited by a lack of substrate, turgor, or Ψ_w gradient. Rather, biochemical changes must have been initiated and resulted in an inhibition of growth that continued for the duration of the experiment. Changes in the acidification of cell walls (32), protein content of cell walls (7), and polyribosome content of cells (20) has been observed a few hours after the imposition of low Ψ_w.

Strength is given to these conclusions by the similarity in the results from the four methods of measuring tissue water status. Not only did turgor behave similarly during transplanting, but the absolute magnitude of the turgor was similar for all measurements. The Ψ_w and Ψ_s also were similar and changed with similar kinetics. Therefore, difficulties described previously that could result from excision (3, 9, 22), dilution of protoplast solution by cell wall solution (affects Ψ_s [5]), or the penetration of the cells with a microcapillary (29) had no significant effect on the conclusions. The conditions under which these factors could become problems have been discussed (3, 29) and precautions were taken to avoid them. In particular, we worked with completely intact tissue (guillotine psychrometer) to avoid excision effects, tissue attached to mature or slowly growing tissue to delay turgor changes after excision (pressure chamber [3, 22, 28]), etiolated seedlings having thin cell walls to minimize significant amounts of contaminating wall solutions (psychrometer), and tissues with cells large enough to be minimally affected by the penetration of a microcapillary (pressure probe).

Cosgrove *et al.* (9–11) and Hsiao and Jing (17) argue against the use of excised tissue to measure turgor in elongating tissue because of a relaxation of the cell walls after the water supply is shut off. The relaxation would cause turgor to be lower than in the intact plant. However, we showed (3, 22) that the relaxation is smaller than indicated by Cosgrove *et al.* (9–11) and that mature or slowly growing tissue attached to the elongating tissue will delay relaxation for times long enough to obtain reliable measurements.

Although the agreement between methods in the present study indicates that excision effects were small enough to ignore (2, 3, 6, 8), the measurements in mature tissue were so different from those in elongating tissue that mature tissue could not be used to infer the turgor in the elongating cells. Thus, in studies of growth, turgor measurements in mature tissue should not be used to indicate the turgor of the enlarging cells (25).

The present work demonstrates that growth in higher plants is more complex than in single cells in direct contact with water. In the large-celled alga *Nitella*, turgor was lost immediately upon exposure to low Ψ_w, and cell elongation was simultaneously inhibited (15). In higher plants, the cells in growing tissues are not in direct contact with free water. They must pull water from a distant xylem through intervening cells that pose a resistance to water movement. Both the availability of water and the geometry of the cells become important. Molz and Boyer (26) and Silk and Wagner (31) considered the effects of geometry and proposed that Ψ_w would need to be significantly below the xylem Ψ_w to extract water at rates that would sustain growth.

When local equilibrium of the Ψ_w between protoplasts and cell walls was assumed, the potential field could be calculated theoretically (26, 31) and measured experimentally (3, 8, 26, 28). Because there is evidence (2, 28) that the field arises from the yielding of the cell walls during enlargement, which prevents turgor from becoming as high as in the absence of growth, the field was considered growth-induced. The presence of the field causes growth to be sensitive not only to turgor as in single cells but also to changes in Ψ_w anywhere in the enlarging tissue. Changes in Ψ_w that occur in the xylem are particularly relevant because the xylem participates in the potential field, forming the initial part of it. Changes in xylem Ψ_w can occur rapidly when the soil Ψ_w changes or transpiration rates vary.

These findings indicate that although growth can be inhibited by low turgor, it also can be inhibited by factors other than turgor loss when tissue Ψ_w decreases. Because the experiments involved intact plants and conditions that often occur in nature, these factors probably operate frequently. We propose that the factor initiating the inhibition was the decreased Ψ_w of the xylem and nearby cells that disrupted the growth-

induced Ψ_w necessary for water to enter the elongating tissues. Without water entry, growth could not occur in spite of the high availability of substrate and the constancy of turgor in the bulk of the tissue.

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