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Rapid Changes in Cell Wall Yielding of Elongating *Begonia argenteo-guttata* L. Leaves in Response to Changes in Plant Water Status[1]

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ABSTRACT

Elongation and epidermal cell turgor (*P*) of *Begonia argenteo-guttata* L. leaves were simultaneously measured to determine the wall-yielding behavior of growing leaf cells in response to changes in plant water status. Rapid changes in plant water status were imposed by irrigating the rooting media with solutions of −0.20 and −0.30 MPa mannitol. These treatments caused decreases in *P* of 0.09 and 0.17 MPa, respectively. The decreases in *P* were complete within 10 min, and *P* did not change thereafter. Following treatments, leaf elongation was nil for periods of 25 to 38 min. Subsequently, elongation recovered to steady rates that were 45 or 75% lower than in the well-watered controls. Leaves of plants that were pretreated with −0.30 MPa of mannitol and rewatered showed an increase in *P* of 0.19 MPa, which was complete within 15 min; *P* did not change thereafter. Rewatering caused a several-fold increase in leaf elongation rates, which subsequently declined while *P* was increasing, to reach steady rates similar to that of the controls. Several estimates of elastic deformation indicated that most of the elongation responses to altered *P* were due to changes in irreversible deformation. The results showed that the initial effects of changes in *P* on leaf elongation were partially compensated for by changes in the cell wall-yielding properties. We conclude that linear relationships between *P* and adjusted growth rates are not necessarily indicative of constant wall-yielding properties. Instead, these relationships may reflect the effect of *P* on wall-loosening processes.

Among plant processes, leaf expansion is one of the most influenced by changes in plant water potential (1, 2, 14). The expansion of leaves occurs when irreversible extension of cell wall by *P*[3] is followed by water uptake (3, 6). The present theory for cell wall extension during growth describes the dependence of irreversible wall deformation (*G*) on cell *P* and two yielding properties of the wall that resist the force exerted by *P* on the wall:

$$G = m(P - Y) \quad (1)$$

where m is the extensibility (an inverse viscosity) and Y is an empirical yield threshold (13, 18). All terms are under metabolic control. This equation has seen broad use in estimating wall yielding of expanding cells, and can be extrapolated to multicellular tissues (e.g. ref. 4) and organs such as leaves (e.g. ref. 5) when experiments are short term (21). Rapid growth responses to changes in water status and linear relationships between growth rate and *P* suggested that changes in growth were caused by changes in *P* (1, 2) and that m and Y were constant during the changes in plant water status required to develop the elongation/*P* relationship (5, 9, 19, 21). The frequent observation of apparent *P* maintenance (via osmotic adjustment) in the presence of leaf growth inhibition implicates changes, albeit slow, in wall yielding (e.g. refs. 9, 20, 21, 23, 31). However, some question remains about the measurements of *P* in these studies (4, 7, 8). Currently, the most direct and least ambiguous measurement of *P* of expanding cells is obtained by careful use of the pressure probe technique (32). When this technique has been used with *Nitella* internodes (13) and corn roots (15), the results indicated that step changes in *P* were followed by rapid adjustment of wall yielding that tended to maintain the rate of growth.

When the pressure probe was used to determine epidermal cell *P* in expanding grape leaves, Shackel et al. (29) found no response of growth to stepwise increases in *P*. This is consistent with the tendency for self-stabilization of growth following *P* perturbations (11, 13), but appears to contradict the notion that leaf growth is highly sensitive to changes in plant water potential. However, Shackel et al. (29) only increased *P* in well-watered plants and did not investigate water deficits. Furthermore, studies with leaves have not attempted to address the role of elastic deformations that tend to confound analysis of growth responses to *P* perturbations (26).

In this study, we estimated the elastic responses and determined the wall-yielding behavior following treatments that caused rapid changes in plant water status. Continuous measurements of leaf elongation and simultaneous and in situ measurements of cell *P* allowed us to identify rapid adjustment in the wall-yielding properties that partially compensated for the initial effect of changes in *P* on leaf elongation.

MATERIALS AND METHODS

Growing Conditions

Begonia argenteo-guttata plants were grown from rooted cuttings in 550-mL pots in a mixture of sphagnum peat

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[3] Abbreviations: *P*, turgor; LVDT, linear variable differential transformer.

moss:vermiculite:perlite (2:1:1) in a growth chamber under controlled environmental conditions (14-h photoperiod and day/night conditions of 25/18 ± 0.5°C air temperature, 40/70 ± 2.5% RH). Halogen and metal halide lamps supplied approximately 400 μmol m^{-2} s^{-1} PPFD at the leaf level. The plants were watered daily with one-fourth strength Hoagland solution. A plant having seven or eight fully expanded leaves was used for each experiment and discarded after the completion of the experiment. Measurements were made on rapidly expanding or fully expanded leaves (midvein lengths of 67–73 and 138–145 mm, respectively).

Experimental Conditions

Six hours after the initiation of the light period, plants were transported to the laboratory (air temperature 27 ± 3°C and 35 ± 7% RH). The pot was fixed to a custom vibration-free table, and the experimental leaf was positioned in a Plexiglas chamber (115 mL). The chamber was supplied with 240 μmol m^{-2} s^{-1} PPFD from Vita lights (Duro-Test Corp, Fairfield, NJ) and conditioned air (27 ± 0.5°C and 70 ± 2.0% RH) with a flow rate of 150 mL min^{-1}.

Growth Measurements

Instantaneous measurements of growth were made along the leaf midvein using a LVDT (Schaevitz Engineering, Pennsauken, NJ). The petiole adjacent to the lamina was immobilized with respect to the LVDT. The tip of the leaf midvein was connected with the LVDT via kevlar fiber (Edmund Scientific Co., Barrington, NJ), which was attached to the leaf tip using a small alligator clamp cushioned with mounting tape to avoid damaging the leaf. The LVDT output was insensitive to changes in air temperature and air RH when the kevlar fiber was attached directly to the Plexiglas chamber rather than to the leaf tip. Growth occurred throughout the length of the midvein. The relative position of the maximum rate of elongation varied among and within leaves, but exhibited no consistent pattern (28). Relative elongation rates were calculated from the leaf elongation versus time relation using a five-point linear differentiation formula with data input at 1-min intervals.

P Measurements

In situ measurements of cell *P* were made using the pressure microprobe technique (32). All *P* measurements were made in the abaxial epidermis near the center (±5 mm) of the midvein region along the axis in which growth was measured. In growing leaves, these cells were approximately 60 μm long and 33 μm in width and depth, with the longer axis parallel to the leaf midvein. In fully expanded leaves, the cells were approximately 135 μm long and 35 μm in width and depth.

After beveling as described by Shackel et al. (29), the tips of the microcapillaries had ellipsoidal openings that were 1.5 to 3 μm in the major axis and 1 to 2 μm in the minor axis. Opening dimensions smaller than these resulted in frequent plugging of the tips, whereas larger dimensions usually resulted in buckling of the wall of the target cell (29). An aperture 5 mm in diameter was made in the top of the leaf chamber to allow observation of and access to the epidermal cells. The cells were viewed at ×600 using an industrial microscope equipped with a vertical illuminator and a long working distance objective. The microscope could be moved to view cells located at different positions along the leaf midrib without disturbing the measurements of leaf elongation.

The oil pressure in the microcapillary before entering a cell was 0.15 to 0.25 MPa lower than the anticipated *P* of the cell. By increasing the pressure in the microcapillary, the meniscus was brought close to the cell surface such that the volume of cell sap within the microcapillary was less than 0.05% of the cell volume. Stable *P* measurements could be maintained for 10 to 15 min. Prolonged measurements increased the frequency of tip plugging. Therefore, after 2 to 3 min of stable measurement, the tip was withdrawn and used to measure *P* of another cell. During the measurements, the oil/sap meniscus could easily be moved in both directions with changes in the capillary pressure of 0.01 to 0.02 MPa.

Treatments

To change the plant water status, pots were irrigated with 500 mL of 82.07 or 123.10 mM mannitol solutions that had solute potentials of −0.20 and −0.30 MPa, respectively. These solutions were delivered in a period of 3 to 5 min. In some experiments, treatment with mannitol solutions was followed by the addition of 700 mL of deionized water, which was also added to the pots in a period of 3 to 5 min. Drainage from the pots collected 1 to 2 min after addition of mannitol solutions or water had solute potentials similar to that of the added solutions or water, respectively.

In some experiments, apical shoot segments (leaf petioles could not withstand the pressure required for sealing in the pressure chamber) were excised and sealed in a pressure chamber 2 h after treatment with −0.4 MPa (164 mM) mannitol to test for the entry of osmoticum into the apoplast. Xylem sap was collected with the pressure chamber as described by Cosgrove and Cleland (8). Ten-microliter aliquots of xylem sap were used for the determination of carbohydrates by GLC of the trimethylsilyl derivatives of the methyl glycosides. Samples were derivatized and analyzed as described by Komalavilas et al. (16)

RESULTS

Under constant experimental conditions, *P* of abaxial epidermal cells along the leaf midvein remained at 0.52 (SD = ± 0.02) MPa for approximately 5 h (Fig. 1). During this period, the leaf elongated 1.9 mm, with steady elongation rates of 0.6 to 0.7% h^{-1}. Elongation rates within this range were also measured in the growth chamber at similar times of the day. After 5 h, the elongation rates begin to decline. Therefore, we completed all experiments within this period.

Treatment of the potting mixture with −0.20 MPa mannitol caused a decrease in *P* of 0.12 MPa (Fig. 2A). The change in *P* was essentially complete within 10 min of the initiation of mannitol treatment. During the next 2 h, *P* remained at approximately 0.40 MPa. The elongation rate decreased from

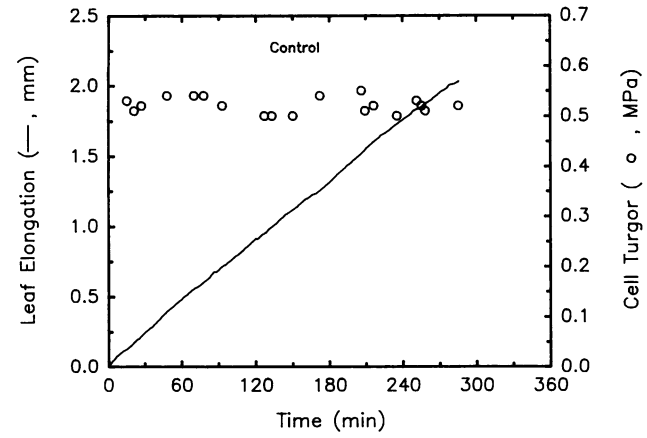

Figure 1. *P* of abaxial epidermal cells and midvein elongation of a representative control leaf of *Begonia* under experimental conditions. Initial leaf length was 70 mm. Initial time (0 min) was approximately 1 h after transporting the plant from the growth chamber to the laboratory. Each point (O) represents the pressure of a single cell.

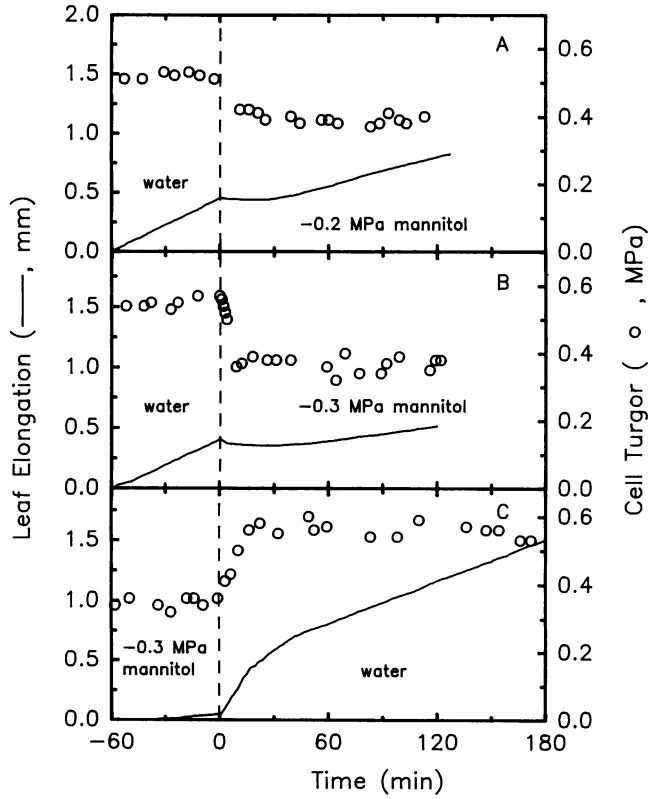

Figure 2. Epidermal cell *P* and leaf elongation of a 70 mm long *Begonia* leaf. A, Before and after −0.20-MPa mannitol treatment of rooting media; B, before and after −0.30-MPa mannitol treatment of rooting media; C, before and after rewatering rooting media that had been pretreated for 2 h with −0.30 MPa mannitol. Initial time (−60 min) was approximately 1 h after transporting the plant from the growth chamber to the laboratory. Each point (O) represents the pressure of a single cell.

0.63 to 0% h^{-1} or slightly negative values within 2 to 3 min of the initiation of mannitol treatment. After approximately 20 min of no expansion, growth recovered gradually to a steady elongation rate of 0.40% h^{-1}, attained approximately 45 min after the treatment. This rate of elongation was maintained for over 90 min (Fig. 2A).

When the root media was treated with −0.30 MPa mannitol, *P* decreased 0.20 MPa (Fig. 2B). The change in *P* began immediately and was complete within 10 min of the initiation of mannitol treatment. *P* remained low during the next 2 h. Leaf elongation was nil or negative for more than 30 min. After this period, growth recovered gradually to a steady elongation rate of 0.20% h^{-1}, attained approximately 50 min after treatment (Fig. 2B).

To test the reversibility of the changes in *P* and elongation rate, plants were rewatered 2 h after being treated with −0.30 MPa mannitol. Rewatering caused an increase in *P* from 0.35 to 0.55 MPa (Fig. 2C), essentially the same *P* observed under well-watered conditions (cf. Figs. 1 and 2, A and B). Rewatering also caused a rapid elongation of the leaf (Fig. 2C), attaining rates of approximately 2.2% h^{-1}. This rate was approximately 3 times greater than that under continually well-watered conditions, and occurred before the completion of the increase in *P*. Approximately 15 min after the initiation of rewatering, the rate of elongation rapidly declined, although no decrease in *P* was observed. Finally, elongation rate reached a steady value of 0.6% h^{-1} (Fig. 2C), which was maintained for over 90 min.

These experiments were repeated three to six times, with similar results each time. The relation between the mean values of *P* and the adjusted rates of elongation (Table I) was positive and linear ($r^2 = 0.95$), suggesting a constant elongation/*P* relation. However, the cessation of growth for 25 and 38 min (for −0.2 and −0.3 MPa treatments, respectively) indicated that during well-watered conditions, *Y* was between the steady-state *P* values measured before and after treatment (Table I).

The estimation of the time course of changes in *P* from data obtained in several cells was confirmed by continuous measurement of *P* in a single cell. These measurements were difficult because contraction and expansion of the tissue during *P* changes tended to displace the cell in relation to the microprobe, resulting in loss of the meniscus or in plugging of the tip. Through delicate movements of the microprobe, it

Table I. *Steady Cell P Values, Periods without Elongation after the Completion of the Decrease in P, and Steady Rates of Elongation for Begonia Leaves before and after Mannitol Treatments to Root Systems*

Means ± SD of *n* experiments.

Treatment	Cell *P*	Period with No Growth (±0.05% h^{-1})	Elongation Rate
	MPa	*min*	*%·h⁻¹*
Water	0.53 ± 0.02		0.66 ± 0.04 (9)
−0.2 MPa mannitol	0.44 ± 0.04	25 ± 8	0.36 ± 0.11 (5)
−0.3 MPa mannitol	0.36 ± 0.02	38 ± 10	0.16 ± 0.04 (6)
Rewater	0.55 ± 0.01		0.62 ± 0.07 (3)

was sometimes possible to maintain a freely moving meniscus during the changes in P following treatments. Changes in cell P following step decreases or increases in the water potential of the root media showed the same kinetics and magnitude as those estimated from measurements in several cells (Fig. 3, A and B), although a freely moving meniscus could not be maintained long enough to confirm a new stable P value.

If significant mannitol entry had occurred, epidermal cell P would increase following the initial decrease, but we never observed P recovery (Figs. 2 and 3). Two hours after treatment, the concentration of mannitol in control and −0.4 MPa-treated leaves was 0 and 2.7 mM (SD = ±1.7, n = 3), respectively. This corresponds to less than 0.01 MPa of osmoticum present in the apoplast of plants treated with a greater concentration of mannitol than that used in the growth experiments. Thus, the pattern of leaf elongation in response to mannitol treatment cannot be attributed to an artifact of mannitol entry and transport to the leaves.

Because unequivocal separation of reversible deformation is experimentally difficult in the intact system, the elastic response to changes in leaf P was estimated by several approaches. First, elastic contraction following mannitol treatment was estimated simply as the decrease in the length

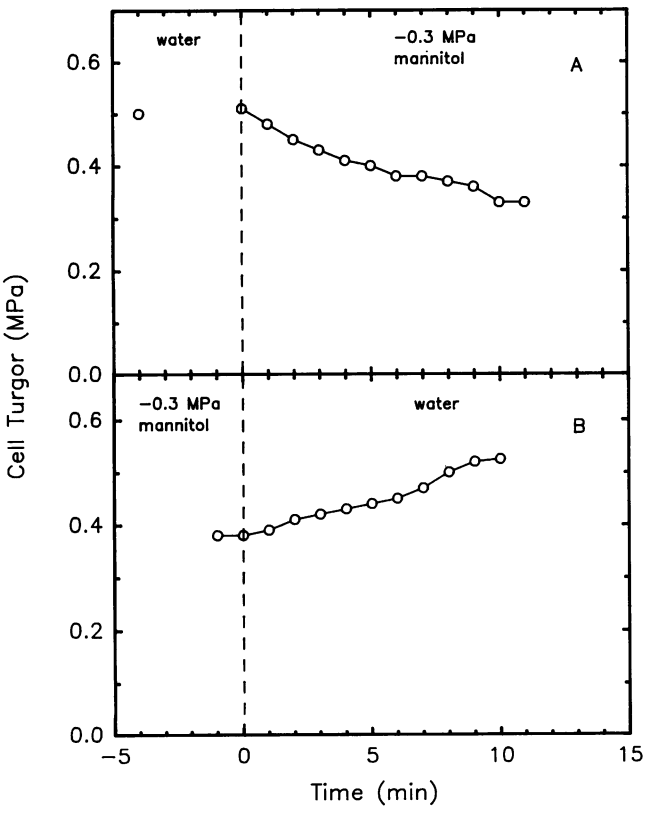

Figure 3. Changes in cell P within the same cell following −0.30-MPa mannitol treatment (A) or following rewatering of plants previously treated for 2 h with −0.30 MPa of mannitol (B). Initial time (−60 min) was approximately 1 h after transporting the plant from the growth chamber to the laboratory. Symbols (O) are arbitrarily placed over a continuously monitored signal.

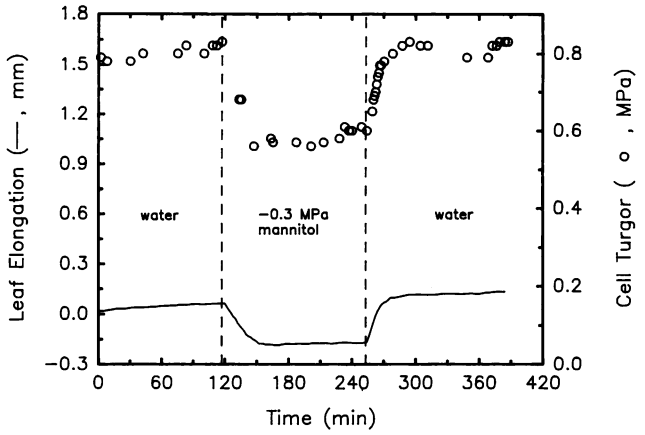

Figure 4. P of abaxial epidermal cell P and leaf elongation of a 140 mm long (mature, nongrowing) *Begonia* leaf before and after −0.30-MPa mannitol treatment and after rewatering of rooting media. Initial time (0 min) was approximately 1 h after transporting the plant from the growth chamber to the laboratory. Each point (O) represents the pressure of a single cell.

of young leaves. Second, elastic expansion following rewatering of young leaves was estimated as the difference between the observed elongation and the elongation that could be attributed to the "adjusted" rate of elongation (i.e. the final steady rate attained after rewatering). Third, measurements of P and leaf length were made in nongrowing leaves where the confounding growth responses could be avoided (Fig. 4).

By definition, relative elastic contraction (immediate and retarded) should be similar to relative elastic expansion. To test this, the magnitudes of elastic contraction and expansion were divided by the respective changes in P (data from experiments described in Figs. 2 and 4). The values of these quotients (summarized in Table II) indicated that the contraction for a unit decrease in P in young leaves was 3 to 5 times smaller than the expansion for a unit increase in P. In contrast, contraction and expansion per unit P were similar in mature leaves. Relative expansion of young leaves was also 3-fold greater than in mature leaves. Thus, all of the estimates of elastic deformation following the decrease in P

Table II. *Elastic Expansion and Contraction of Begonia Leaves in Response to P Changes*

Estimates of elastic deformation from the decrease in leaf length (contraction) and from the increase in leaf length that cannot be attributed to steady elongation rates (expansion) for leaves exposed to rapid changes in water status. Means ± SD of n experiments.

Leaf	Elastic Deformation	
	mm MPa^{-1}	% MPa^{-1}
Young		
Contraction	−0.40 ± 0.20	−0.66 ± 0.33 (5)
Expansion	2.01 ± 0.38	3.34 ± 0.64 (4)
Mature		
Contraction	−1.11 ± 0.30	0.93 ± 0.25 (3)
Expansion	1.07 ± 0.38	0.89 ± 0.32 (3)

were too small to account for the rapid elongation of the leaf following rewatering.

DISCUSSION

The treatments that we used to alter plant water status caused changes in epidermal *P* and transient and steady-state changes in leaf elongation rates. Following rapid reductions in *P*, leaf expansion recovered without an accompanying increase in *P*. Following pretreatment at low *P*, rewatering caused leaf expansion to increase to rates that were 3-fold greater than those observed under control conditions, although cell *P* did not differ in the control and rewatered plants. In addition, elongation in the rewatering experiment subsequently decreased to control rates without a corresponding decrease in cell *P*. These manifest alterations in the elongation/*P* relation that occurred upon both increases and decreases in *P* indicated that the initial effects of *P* on elongation were partially compensated for by rapid adjustments of cell wall-yielding properties.

The changes in the elongation/*P* relation we report are not attributable to elastic changes in leaf length. Elastic deformation cannot be invoked to explain the post-treatment recovery of growth at constant low *P* nor the difference between the magnitude of leaf contraction and expansion caused by the observed changes in *P*. For elastic responses to account for the cessation of elongation upon *P* decreases, very large and prolonged elastic contraction would be required. Because the difference between the expansion and contraction coefficients was greater than 100%, the magnitude of retarded elastic deformation would need to be similar to the magnitude of instantaneous elastic contraction observed during the decrease in *P* to account for the changes in the elongation/*P* relation observed following mannitol treatment. If retarded elasticity was responsible for the cessation of elongation, its effect must outlast the changes in *P* for 20 to 40 min. Both of these would be highly unusual characteristics. For example, retarded elastic responses observed in multiaxial extensibility studies with *Nitella* (22) were not larger than 25% of the immediate elastic response and were essentially complete in 5 min. Also, in nongrowing leaves of *Begonia*, the changes in *P* occurred simultaneously to the changes in length, and no significant deformation could be detected following the completion of the change in *P*.

We estimated total elastic deformation by several methods, all of which were inadequate to account for the high growth rates observed upon rewatering. Furthermore, in contrast to growing leaves, the contraction of nongrowing leaves in response to a decrease in *P* was similar to the elongation of the leaf in response to the increase in *P*. This indicates that when deformation is solely elastic, the response is completely reversible.

The changes in *P* observed in epidermal cells could have been different than the changes occurring in inner cells of the midvein. However, for this to account for the elongation responses would require the decrease in *P* in inner cells of growing leaves to have been smaller than its increase upon rewatering. This seems unlikely because the changes in the epidermis *P* were completely reversible. Also, the changes in *P* of mature leaves were apparently completely reversible because epidermal cell *P* and elongation changes were completely reversible. Even if hysteresis of *P* occurred, it would still be uncertain how changes in inner cell *P* caused a change in stress in the outer epidermal wall that appears to limit organ expansion in leaves and stems (10, 17, 30).

Nonami and Boyer (24) showed that the growth of soybean hypocotyls transplanted to low water potential media also initially ceased and later partially recovered. The initial inhibition of growth was due to a collapse of the growth-induced water potential gradient. Although the gradient was reestablished, growth remained depressed for an extended period before partially recovering. The recovery of growth was not attributable to any detectable changes in water transport or *P*. A similar phenomenon may occur in *Begonia* plants when subjected to low water potential media.

The recovery of leaf elongation at low *P* and the rapid rates of elongation observed upon rewatering may reflect the same changes in cell wall yielding. The adjustment of elongation rates following rapid changes in *P* was at least partially attributable to changes in *Y*. Clearly, the instantaneous relation between *P* and elongation was determined by values of *Y* different than those estimated from the linear relation between *P* and "adjusted" (in this case, upon recovery of growth after mannitol treatment) rates of elongation. When *P* decreased 0.09 MPa after addition of 0.20 M mannitol, elongation ceased for 25 min, indicating that the effective *P* for growth (*P-Y*) was less than 0.09 MPa. In contrast, extrapolating from the relation between steady *P* and the adjusted rates of elongation (see, e.g., ref. 21) produces an estimated *Y* of 0.31 MPa, or 0.22 MPa below the *P* values measured in control plants. The recovery of growth at a constant *P* shown here and earlier in stems (25) and *Nitella* internode cells (13) is also inconsistent with a single value of *Y*. Thus, our results support the hypothesis that the conventional single estimates of *Y* are not the values of *Y* determining the instantaneous rate of growth (13, 25, 30). Instead, these estimates represent critical *P* values (*Pc*) below which *Y* cannot be adjusted rapidly.

Because the effective *P* for growth was smaller than (*P-Pc*), the physical extensibility determining the instantaneous rate of growth must have been greater than the m obtained from the relation between *P* and adjusted rates of elongation (m_a). The severalfold shift in elongation rates observed following pretreatment at low *P* and upon the increase in *P* (Fig. 2C) also indicated a steep elongation/*P* relation. Green et al. (11) proposed earlier that the slope of the relation between *P* and adjusted rates of growth was not the physical extensibility determining the instantaneous rate of growth. Instead, they suggested that the physical extensibility should be determined from the rates of irreversible expansion before and immediately after a *P* shift (m). Green et al. (12, 13) and Okamoto et al. (25) induced rapid changes in *P* of *Nitella* internodes and excised tissue of higher plants, respectively, while reducing the period of elastic changes to between 30 s and 2 min. The quotient between the growth rate shift and the *P* shift gave values of m that were severalfold larger than the values obtained for m_a.

In the intact plants, we could not hasten the rate of increase in *P*. The elongation rates measured after the 15 min required

to change P were most likely substantially adjusted. Nevertheless, we used these rates of elongation to obtain a lower limit for the value of m. Averages of elongation rates and P values measured before and 15 min after rewatering were used to calculate the quotient between the growth rate shift and the P shift. The value of m estimated using this approach was 0.12 h^{-1} MPa^{-1}, approximately 4 times larger than the value of m_a, which was 0.029 h^{-1} MPa^{-1}.

Our estimate of m was smaller than the 1.0 and 0.5 h^{-1} MPa^{-1} reported by Green et al. (13) and Okamoto et al. (25), respectively. In addition to our estimate being low, the differences in the results may reflect differences between tissues in their capacity for wall expansion. Green et al. (11) observed that incubation of rye coleoptiles with IAA augmented the initial growth response to an increase in P. Also, in several studies, the growth rate shift in response to a step increase in P was greater when the initial steady-state P was markedly increased (11, 12, 25). This indicates that m could vary with changes in P. Thus, in our study, adjustment of growth may have also been partly mediated by changes in m.

In leaves, the recent observation of the same rate of elongation at different turgors within 30 min in grape (29), and the present analyses showing reversibility and little elastic contribution to changes in the elongation/P relation, provide strong evidence of rapidly dynamic wall-yielding properties. Similar results with other systems (e.g. refs. 1, 13, 15) indicate that rapid and self-stabilizing changes in the elongation/P relation are widespread, if not general, and that in addition to being under continuous metabolic control (13, 25, 27), these properties are to some extent P dependent. Because P is highly dynamic and the changes in wall yielding can occur within 15 to 30 min, physical models of wall expansion may be inadequate to describe growth phenomena unless changes in wall-yielding properties can be described by relating them to wall-loosening or wall-hardening processes (27, 29).

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