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Estimation of the Volumetric Elastic Modulus and Membrane Hydraulic Conductivity of Willow Sieve Tubes[1]

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ABSTRACT

Severed aphid stylets were used to follow the kinetics of sieve tube turgor and osmotic pressure (π) responses following step changes in water potential applied to the cambial surface of willow (*Salix exigua* Nutt.) bark strips. The kinetics of the turgor response were monitored with a pressure transducer. In separate experiments, the kinetics of the π response were followed by freezing point determinations on stylet exudate. The sieve tube volumetric elastic modulus in the bark strips was about 21 bars, but may be higher in intact stems. The membrane hydraulic conductivity was about 5×10^{-8} centimeters per second per bar; several factors make it difficult to estimate its value accurately. Differences in the turgor pressure (P) and π responses, as well as the relatively more rapid initial turgor response to a water potential (Ψ) change, suggested a time-dependent component in sieve tube wall elasticity.

Our observations were generally not supportive of the idea that sieve tubes might osmoregulate. However, the bark strip system may not be suitable for addressing that question.

Separate measurements of Ψ, P, and π demonstrate that the relationship predicted by the fundamental cell water potential equation, $\Psi = P - \pi$, is applicable within experimental error (± 0.4 bar) to sieve tube water relations.

The rate of net water movement into or out of a plant cell is determined to a large extent by the Lp[4] of its plasma membrane and by the ϵ of its surrounding cell wall (2). In the case of the sieve tube, knowledge of these parameters is essential not only to an adequate understanding of those aspects of cell water relations common to all plant cells, but to characterizing the sieve tube's function as the conduit for long distance nutrient transport. The appreciable elasticity of the sieve tube wall has been inferred for some time from observations on sieve tube exudation (4). However, it is experimentally difficult to quantify these two parameters for higher plant cells, particularly for a specific cell type embedded in a tissue composed of several cell types (6). Some progress has nevertheless been made by Lee (10) and by Sovonick-Dunford *et al.* (11) in the case of sieve tubes in the secondary phloem of trees. Although the experimental approaches were quite different in the two studies, both relied on observations made on bulk volume changes of the secondary phloem. Their interpretation of the observed volume changes necessarily depended on assumptions regarding the uniformity of cell properties in the secondary phloem.

The approach we employed to estimating these parameters (the use of a pressure transducer sealed to severed aphid stylets) is similar in basic concept to the 'pressure-probe' technique of Zimmerman *et al.* (14), which is more suited to single cell measurements. The results suggest some time-dependence in the elastic properties of the sieve tube wall, but gave values of the elastic modulus and membrane hydraulic conductivity which are reasonably similar to those obtained by Lee (10) and by Sovonick-Dunford *et al.* (11).

MATERIALS AND METHODS

Plants and Aphids. Colonies of the giant willow aphid (*Tuberolachnus salignus* Gmelin) were maintained on saplings of *Salix exigua* Nutt. grown in the laboratory under two 400-w metal halide lamps. Illumination (PAR) was approximately 200 μE m^{-2} s^{-1}. Experimental bark strips, about 1.5 cm × 7 cm × 1 mm, were removed from 3- to 5-year-old branches of *Salix exigua* and sealed into plexiglass holders using a 1:4 mixture of lanolin and paraffin. The holders had a volume of about 3 to 5 ml and allowed constant irrigation of the cambial surface with experimental solutions. Ten to 15 willow aphids were caged on the bark strip overnight, during which time Higinbotham's 1X solution (5), composed of 1 mM KCl, 1 mM $Ca(NO_3)_2$, 0.25 mM $MgSO_4$, 0.904 mM NaH_2PO_4 at pH 5.7, was circulated past the cambial surface. Stylets were cut with a razor blade fragment the next morning.

Measurement of Osmotic and Turgor Potentials. Manometric measurements of sieve tube turgor were obtained as before (13). Basically, this involved using ethylcyanoacrylate adhesive to seal a glass capillary, flamed shut at the opposite end, over an exuding stylet. In the present measurements, obtained in Pullman, a correction was applied to the compression of the air column in the manometer to account for the reduction in barometric pressure due to elevation. This correction had not been required for our earlier measurements taken at a much lower elevation in Athens, GA. After obtaining the pressure measurement, the manometer was broken off under mineral oil and some stylet exudate was collected with a fine-tipped pipet. Exudate osmotic pressures were measured with a nanoliter osmometer (Clifton Technical Physics, Hartford, NY) by freezing point depression.

Owing to its relative imprecision and the volume of exudate flow required, the capillary manometer was not a suitable device for following pressure changes. Therefore, a pressure transducer (model XCQ-050, Kulite Semiconductors, Inc., 1.25 mm o.d.) was used to follow the kinetics of the turgor response to step changes in the water potential. The transducer was epoxied into a glass capillary that had been drawn to a fine tip, approximately 0.1 mm in diameter, at the other end. The capillary (approxi-

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[4] Abbreviations: Lp, membrane hydraulic conductivity; ϵ, volumetric elastic modulus; Ψ, water potential; P, turgor pressure; π, osmotic pressure.

mately 1–2 mm^3) was then filled under vacuum with Dow Corning 200 silicone fluid. As in the case of the manometric measurements, the capillary was sealed to the stylet with ethylcyanoacrylate adhesive. However, owing to the rapid pressure buildup (no air space was present in the capillary/transducer assembly), it was more difficult to obtain a good seal on the bark. Sealing to a glue surface was more reliable, so the problem was remedied by first sealing a glass capillary manometer around the stylet (as above), breaking it off close to the stem, and trimming the surface of the manometer and surrounding adhesive to give a flat surface. A water droplet was placed on the manometer-glue surface and the tip of the capillary-transducer device was advanced into the droplet by a micromanipulator. Any air bubbles in the manometer tip were removed by warming, which expanded the silicone fluid and forced air bubbles from the capillary tip. The capillary tip of the transducer device was then pushed against the glue surface, directly over the exuding stylet. The water was removed and quickly replaced with ethylcyanoacrylate, followed by a spray of accelerator (Quick Filler Setter, Permabond International Corp). To eliminate pressure fluctuations caused by thermal expansion or contraction of the silicone fluid, a sleeve of foam rubber, about 3 cm in diameter, was slipped over the capillary-transducer assembly, followed by additional foam pieces to block any remaining spaces around the capillary. In most experiments, a thermocouple glued to the body of the capillary was used to monitor temperature changes of the silicone fluid. Temperature changes down to about 0.1 to 0.05°C min^{-1} affected the pressure reading. However, the insulation kept rates of temperature change below this. The voltage input for the transducer was provided by a 1.35 v mercury battery. Voltage output was followed with a Keithley 610B electrometer and a strip chart recorder.

The criteria for a successful pressure measurement were (a) after major temperature fluctuations ceased (they were quite marked while spraying the accelerator) the pressure increased quickly and smoothly to a constant value and (b) after getting the insulation in place, the pressure remained constant for at least 15 min. During an experiment, suspect pressure readings were checked by gently warming the capillary-transducer assembly. Since, after longer periods, incorrect readings often arose from plugging of the stylet (usually indicated by a slow decline in pressure), the pressure increase caused by warming would quickly drop back to the initial pressure if the stylet were open.

Although only a very small volume flow should be required for the transducer response to a pressure change, it nevertheless seemed conceivable that the stylet's resistance to flow could affect the response kinetics during rapid turgor variation. This was checked in two experiments in which the capillary-transducer apparatus was pulled from the stem with the stylet still sealed to the capillary. The stylet and capillary tip were submerged in water at the end of a test tube which supported the capillary-transducer apparatus, and the test tube was placed in a pressurizable container. Step changes in pressure were generated by quickly opening the container after pressurization to about 1 bar with compressed N_2. To be sure that pressure was being sensed via the stylet rather than by compression of the capillary-transducer device, the stylet was later cut off, a layer of glue was applied to seal the opening, and the pressure response was determined again.

The water potential of bark strips was varied in a stepwise manner by flushing 1X nutrient solutions containing appropriate concentrations of mannitol through the bark strip holder. Solution π values were verified from their freezing point depression. The initial 30 to 40 ml were run through quickly to generate an essentially instantaneous change in solution water potential. Following this initial change, the flow rate was slowed to 10 to 20 ml/min.

Similar experiments were run to determine the response of sieve tube osmotic pressure to step changes in the water potential. In these, the stylet exudate was collected under mineral oil. Before collecting a sample, previously accumulated exudate was removed from the stylet and the volume exuding during the next 15 to 30 s was taken for π determination.

Calculation of the Volumetric Elastic Modulus and Membrane Hydraulic Conductivity. Values of ϵ were calculated from the following relationships (2), which assume constant πV and small volume changes:

$$\Delta\Psi = \Delta P - \Delta\pi \quad (1)$$

$$\Delta\pi = -\pi\ \Delta V/V \quad (2)$$

$$\Delta P = \epsilon\ \Delta V/V \quad (3)$$

For a given step change in the water potential ($\Delta\Psi$), $\Delta\pi$ was calculated from equation 1 using the difference (ΔP) between the steady values for P before and after its response to $\Delta\Psi$. Since, at steady state, $\Psi = P - \pi$ (Table I), the fractional volume change of the sieve tube ($\Delta V/V$) could be calculated from equation 2, finally allowing the calculation of ϵ (equation 3). Assumption of constant π during a Ψ change had little effect on the resulting value of ϵ in comparison to variations between experiments.

The Lp was calculated from the half-time of the turgor response to a change in water potential (2)

$$t_{1/2} = \frac{0.693\ V}{ALp(\epsilon + \pi)} \quad (4)$$

where A is the surface area of the cell. The ratio of V/A for a cylinder 10 μm in radius was used in the calculations. (Measurements of the radius of 26 sieve tubes gave a value of 9.4 ± 2.7 μm.)

RESULTS

Comparison of Measured *Versus* Calculated Turgor Pressures. As a test of the accuracy of our P and π measurements, we compared manometrically measured turgor pressures with those calculated from Ψ and π measurements in 18 experiments (Table I).

When comparisons were made between stylets on the same bark strip, the data rarely differed by more than a few tenths of a bar (several comparisons not shown).

Kinetics of the Turgor Response to Step Changes in Water Potential. In the absence of any change in water potential of the solution flowing past the cambial surface, sieve tube turgor (monitored by the pressure transducer) was likewise fairly constant, sometimes showing gradual changes of a few tenths bar over several hours. (Several stylets were monitored under steady Ψ for 4 h; one was followed for 10 h.) The turgor response to a step change in water potential was prompt and followed a smoothly varying time course until the response was complete, usually within about 10 to 20 min (Fig. 1). This response was two orders of magnitude slower than that observed ($t_{1/2} < 1$ s) when a step change in pressure was applied to a stylet, still sealed to the tranducer, after it was pulled from the stem. The response was not due to simple compression of the apparatus, since it disappeared on sealing the stylet.

Except in a few instances when no difference was observed, the 'half-time' for the response (*i.e.* the time for half the remaining pressure change to occur) was shorter for the first half of the turgor change than for the remaining half. For 20 step changes in Ψ, the average half-time for the first half of the turgor change was 3.9 ± 1.9 min, with a range of 1.8 to 8 min. The average time to complete the next one-fourth of the total turgor change (the 'second' half-time) was 6.7 ± 4.0 min. with a range of 2 to

Table I. *Comparison of Sieve Tube Turgors Measured Directly with a Micromanometer with Turgor Pressures Calculated from Exudate Osmotic Pressure and Water Potential Measurements*

The water potential in all experiments was taken to be −0.4 bar, the same as the solution bathing the cambial surface.

π	Calculated P[a]	Measured P	Difference (Calc. − Meas.)
	bars		
8.5	8.1	8.0	0.1
7.7	7.3	6.1	1.2
12.4	12.0	11.7	0.3
5.6	5.2	5.3	−0.1
8.0	7.6	7.2	0.4
8.1	7.7	7.0	0.7
7.9	7.5	7.2	0.3
6.5	6.1	6.0	0.1
5.4[b]	5.0	4.9	0.1
5.4[b]	5.0	5.1	−0.1
6.2	5.8	5.4	0.4
5.3	4.9	4.7	0.2
6.3	5.9	5.7	0.2
5.6	5.2	5.0	0.2
5.5	5.1	5.2	−0.1
6.1	5.7	5.4	0.3
8.4[c]	8.0	6.7	1.3
—[c]	—	6.3	—
—[c]	—	6.2	—
6.8[c]	6.4	6.3	0.1
Mean ± SE 7.0 ± 1.8	6.6 ± 1.8	6.3 ± 1.6	0.3 ± 0.4

[a] $P = \Psi + \pi$.

[b] Stylets 6 mm apart on the same bark strip.

[c] Stylets on the same bark strip.

15 min. Subsequent half-times did not seem to show a further increase, but this was usually difficult to judge accurately. The half-times for a given stylet also sometimes varied appreciably, but within half the above values.

In most of the experiments, Ψ was decreased in steps of −2 bars. However, in four instances where it was increased, there was no indication of any difference in the characteristics of the response, including the shorter 'first' half-time. These responses are included in the 20 cited above.

The extent of the change in turgor pressure was only about two-thirds to three-fourths of that in water potential (Fig. 2, plus observations from two less complete experiments).

For 16 step changes in Ψ, $\epsilon = 27 \pm 21$ bars, and the calculated Lp values were $5.5 \pm 2.1 \times 10^{-8}$ and $3.0 \pm 1.0 \times 10^{-8}$ cm s^{-1} bar^{-1} for the first (3.9 min) and second (6.7 min) half-times, respectively.

Kinetics of the Osmotic Pressure Response to Step Changes in Water Potential. Since two-thirds to three-fourths of the sieve tube water potential change was accounted for by their change in turgor, the expected change in their osmotic pressure was much smaller (*i.e.* the remaining one-third to one-fourth of the water potential changes; see equation 1). For this reason, 4-bar changes in Ψ were used in most of these experiments to improve their accuracy.

The response of π to a step change in water potential (Figs. 1b and 3) was roughly as expected from the turgor measurements (preceding section) in that there was a prompt change in π amounting, on the average, to 38% of the imposed change in water potential. However, there were some unexpected differences. In three experiments, the initial change in π was followed by a prolonged linear change (Figs. 1b and 3), suggesting solute accumulation by the sieve tubes. Nothing comparable was observed in the turgor measurements. In general, the half-time of the π response (about 12 min from instances where it could be estimated with reasonable confidence) appeared to be longer than for at least the first half-time of the turgor response (3.9 ± 1.9 min). Finally, the π response was more erratic in several respects than the turgor response. Particularly after Ψ changes, π values seemed more likely to be irregular, both in the sense of sometimes being variable (Fig. 3, b and d), or sluggish in responding to the Ψ change (Fig. 3, a–d). In one case (Fig. 3d), the rapidity of the π response was very different in successive Ψ changes. These differences between P and π responses were evident in several other, less complete, experiments. The relative slowness of the π responses was particularly evident when Ψ was changed by only 2 bars.

Surprisingly, in view of the variability noted above, when two stylets were exuding on the same bark strip the kinetics of their π responses were quite similar (Fig. 3, a and c). This encourages some confidence in comparing the π and P kinetic data obtained in one experiment from different stylets on the same bark strip (Fig. 1b).

DISCUSSION

In comparison to our earlier report (13), the accuracy of both the osmotic pressure and water potential values have been improved substantially. Owing to the small sample volumes, we previously had to rely on refractive indices for our estimates of exudate osmotic pressures; sieve tube water potentials were estimated from leaf water potentials measured by dewpoint psychrometry. In the present experiments, exudate osmotic pressures were determined to ± 0.1 bar and, since sieve tube water potential equilibrated fairly rapidly with that of the solution bathing the cambial surface (as shown by the turgor response kinetics; see below), the estimates of sieve tube water potentials should have similar accuracy. That the anticipated accuracy was in fact realized is shown by the agreement between the measured and calculated values for turgor pressures (Table I). The average difference was 0.31 bar; only 3 of the 18 comparisons gave values differing by more than 0.4 bar. Since we estimate the error for turgor measurement (arising from measurement of the length of the compressed air columns) to be ± 0.3 bar or less (13), all but the latter three comparisons of calculated and measured turgor values agree to within the expected experimental error. To our knowledge, this is the only instance where the fundamental water potential equation ($\Psi = P - \pi$) has been verified experimentally for a higher plant cell by independent measurements of each component. (It should be noted that the system is not quite in equilibrium during exudate collection. However, with $Lp = 5 \times 10^{-8}$ cm s^{-1} bar^{-1}, a velocity of 5 cm min^{-1}, and the observed sieve plate pore diameter of about 2 um, the expected $\Delta\Psi$ across the sieve tube plasmalemma would be close to an undetectable 0.1 bar.)

The pressure probe appeared to track quite accurately the time course of turgor changes in the sieve tube. This is shown most directly by the rapid response to step pressure changes applied to a stylet withdrawn from the stem, and is supported by the greater rapidity of the turgor response as compared to the osmotic pressure response to $\Delta\Psi$ changes. Both observations also suggest a negligible effect of the probe chamber's elasticity on the estimations of sieve tube wall elasticity. The latter problem is not to be expected in any event, given the low resistance to flow in sieve tubes (*i.e.* the stylet senses turgor in a large effective 'cell' volume). Furthermore, while calculated values for ϵ are not presented for the osmotic response experiments, simply the fact that the observed $\Delta\pi$ (about one-third of the imposed $\Delta\Psi$) was close to that predicted for the turgor response experiments (one-third to one-fourth of the imposed $\Delta\Psi$) demonstrates that the two kinds of experiments indicated similar ϵ values.

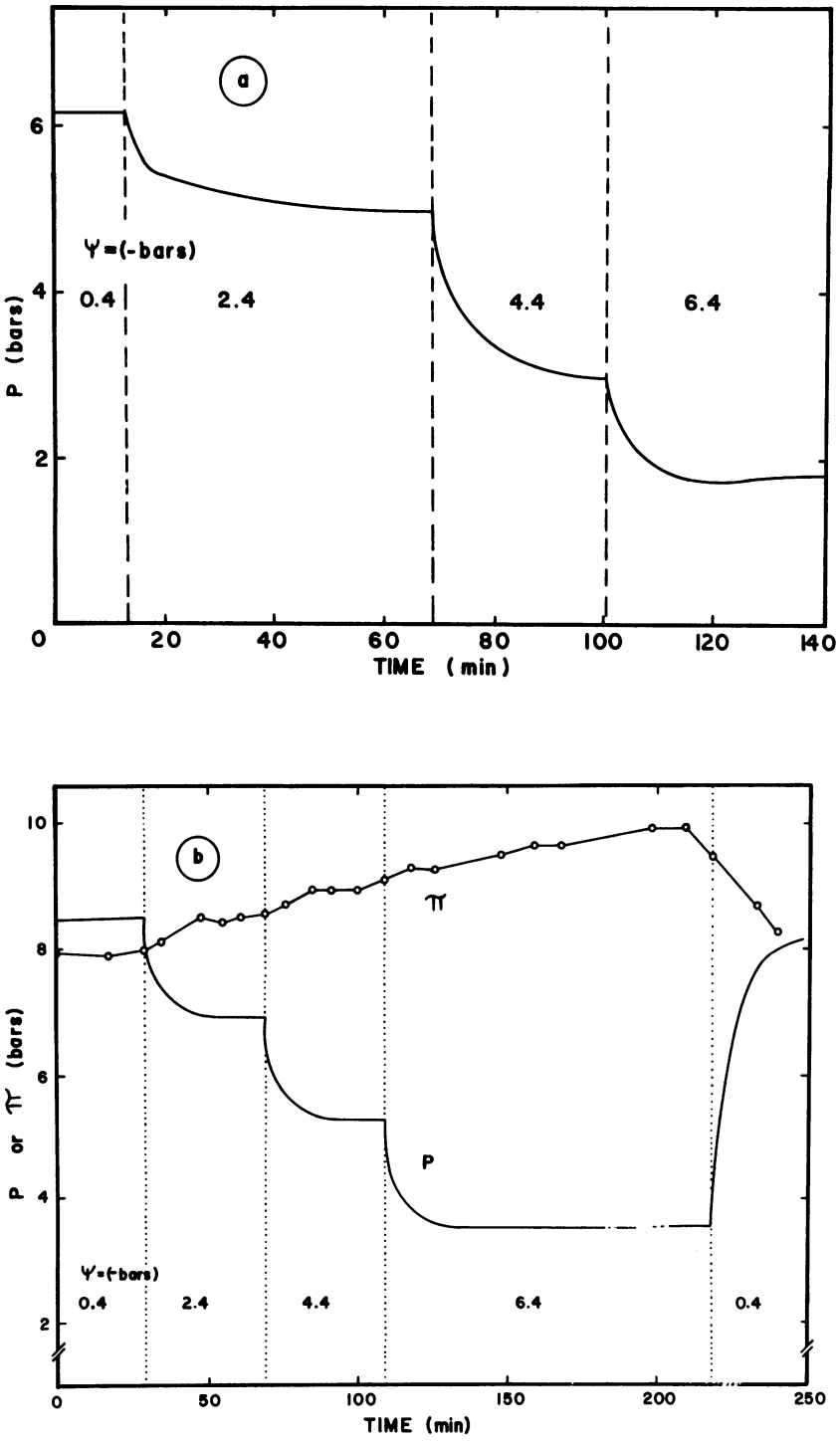

FIG. 1. Two examples of sieve tube turgor responses to step changes in Ψ, as measured by a pressure transducer. b, Two stylets on the same bark strip were used to follow both P and π in the same experiment.

The values obtained for ϵ fall into the low range for plant cell walls (2), indicating that the sieve tube wall in this system has considerable elasticity. Lee (10), who used position tranducers to follow the shrinkage of secondary phloem of ash at various distances from an incision, estimated an elastic modulus of 56 to 73 bars for his material. Sovonick-Dunford *et al.* (11) obtained estimates of ϵ in sections of oak secondary phloem from measured changes in thickness of the sections. Assuming all cell volumes changed similarly, ϵ was 178 bars; if only the sieve tubes were affected, ϵ was 58 bars. Although our values are distinctly lower, considering the range of investigators and experimental approaches, the estimates are reasonably similar.

Some ambiguities arise in the estimation of membrane hydraulic conductivity from the P and π response kinetics. The first concerns the distance of the experimental sieve tube from the cambial surface. Since sieve tubes distant from the surface would not experience a step change in water potential (as assumed in the derivation of equation 4), their turgor (and π) response would be progressively more sluggish with increasing distance from the cambial surface, leading to progressively lower estimates of Lp. In agreement with all but one of our own observations, willow aphids are known to feed on sieve tubes

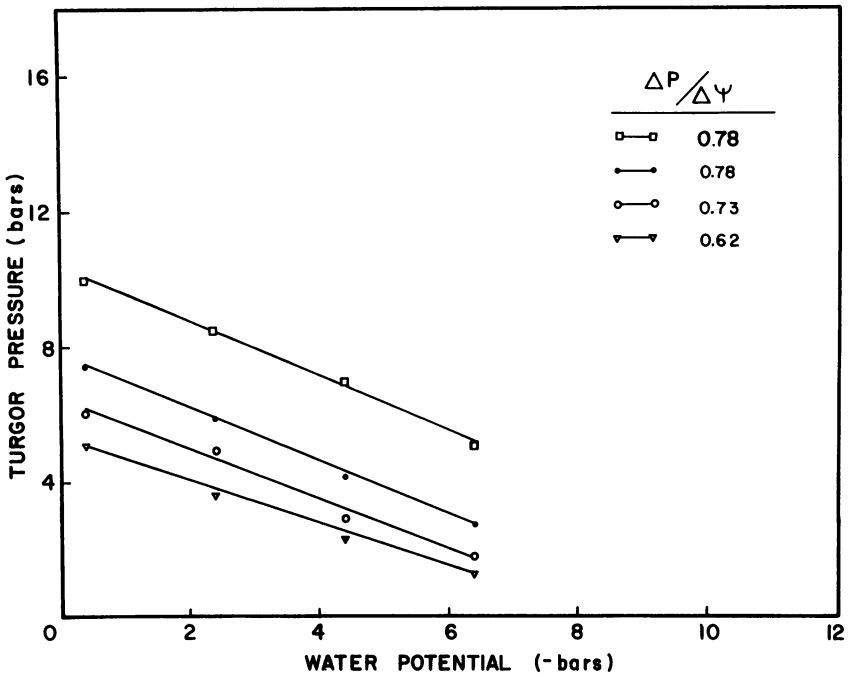

FIG. 2. Summary of equilibrium turgor pressures as a function of Ψ in four separate experiments similar to those in Figure 1.

within the first band of phloem fibers (8, 9), which would place the experimental cells within less than 100 μm from the cambial surface. It seems likely that this is sufficiently close to the surface for these cells to experience a near step change in Ψ (*i.e.* compared to the *P* and π responses), but this is difficult to evaluate with certainty. Klepper *et al.* (7) have estimated an apparent diffusivity of about 1.5×10^{-6} cm^2 s^{-1} for a xylem tension-induced water potential change in the secondary phloem of intact cotton plants. However, our water potential changes were achieved with an applied osmoticum; under these conditions, the diffusion of both water and mannitol would contribute to the propagation of a Ψ change in the apoplast. Dainty has estimated an apparent diffusivity of about 10^{-6} cm^2 s^{-1} for the propagation of a water potential change under these conditions (J Dainty, personal commmunication). Using this figure, the Ψ change 100 μm from the surface would be 50% complete in 2 min, and 75% complete in 8 min (1); at 50 μm, the times would be about 30 s and 2 min, respectively. Thus, the probable half-times for Ψ changes (*i.e.* at positions between 50 and 100 μm from the cambial surface) appear short relative to the observed π and P changes. However, it is clear that there are too many assumptions involved to be confident of this. It is possible that the rate of Ψ change around the experimental sieve tubes may have been sufficiently slow to contribute to an underestimation of *Lp*, and to the longer second half-time of the *P* response.

Variability in the time course of the *P* and π responses, particularly apparent differences between the two, is also a source of uncertainty in the *Lp* calculations. It was clear, in the turgor response, that the kinetics did not follow a single exponential, but was relatively more rapid initially. As pointed out above, distance-dependent Ψ changes may have contributed to this. Differences between the *P* and π responses also complicate interpretations. Given the range of confidence in the π measurements (± 0.1 bar) and the variability between experiments, the real extent of the differences is somewhat uncertain. Transient variations in π, however, would not necessarily be reflected in *P* transients, since the observed turgor at any point along such a low resistance pathway is actually a weighted average of ($\Psi_{sieve\ tube}$ + π) values along the sieve tube near that point (3). Local differences in water movement following a rapid Ψ change might reasonably generate transient, measurable π differences along the lengths of sieve tubes. However, the sluggishness of the π response after a Ψ change, in comparison to the more rapid turgor response, suggests some complexity in the elastic properties of the cell wall. This cannot be ascribed to the often-observed decrease in ε at lower pressures (2), since there was little evidence of variation in ε with turgor (Fig. 2) and the first half-time of the turgor response was shorter for both increased and decreased Ψ. Instead, it appears that the sieve tube wall may have a time-dependent, or viscoelastic, component in its stretching response. During a decrease in Ψ, the essential effect of such viscoelastic behavior could be a higher effective ε during the earlier part of the response than during later parts of the response. As can be seen from equation 4, this also agrees with the observed increase in the half-time during the response (assuming constant *Lp*). Because of the possible time-dependent behavior of ε and the resulting difference in half-times for *P* and π, there is some uncertainty in the calculated values of *Lp*. The somewhat higher *Lp* suggested by the first (shorter) half-time may be due to the higher effective ε during the early part of the response. In any event, the *Lp* values calculated from the two half-times do not differ greatly, and compare favorably with the estimate by Sovonick-Dunford *et al.* (11) of 9.6×10^{-8} cm s^{-1} bar^{-1} for the sieve tube membrane hydraulic conductivity in oak phloem.

Several groups have suggested the possibility that sieve tubes may regulate their turgor. In the case of willow phloem, the idea that sieve tubes might regulate their 'sucrose potential' (12) appears to be one of the earliest experimentally supported suggestions for active turgor regulation in higher plants. However, we did not find convincing support for this idea in our bark strip experiments. Certainly, there was no support provided from the turgor measurements. In the π experiments, the long term π increase sometimes seen (especially of the magnitude in Fig. 3) provides some suggestion that an active π response may have sometimes occurred. It is possible that some of the irregular evidence on this point may arise from the use of bark strips. This is suggested even in the earliest experiments by Weatherly, Peel, and Hill (12), in which they found no long-term π increase (12 h) when stylets were situated on mannitol-stressed bark strips, but a substantial, sustained π increase by stylet exudate on stem

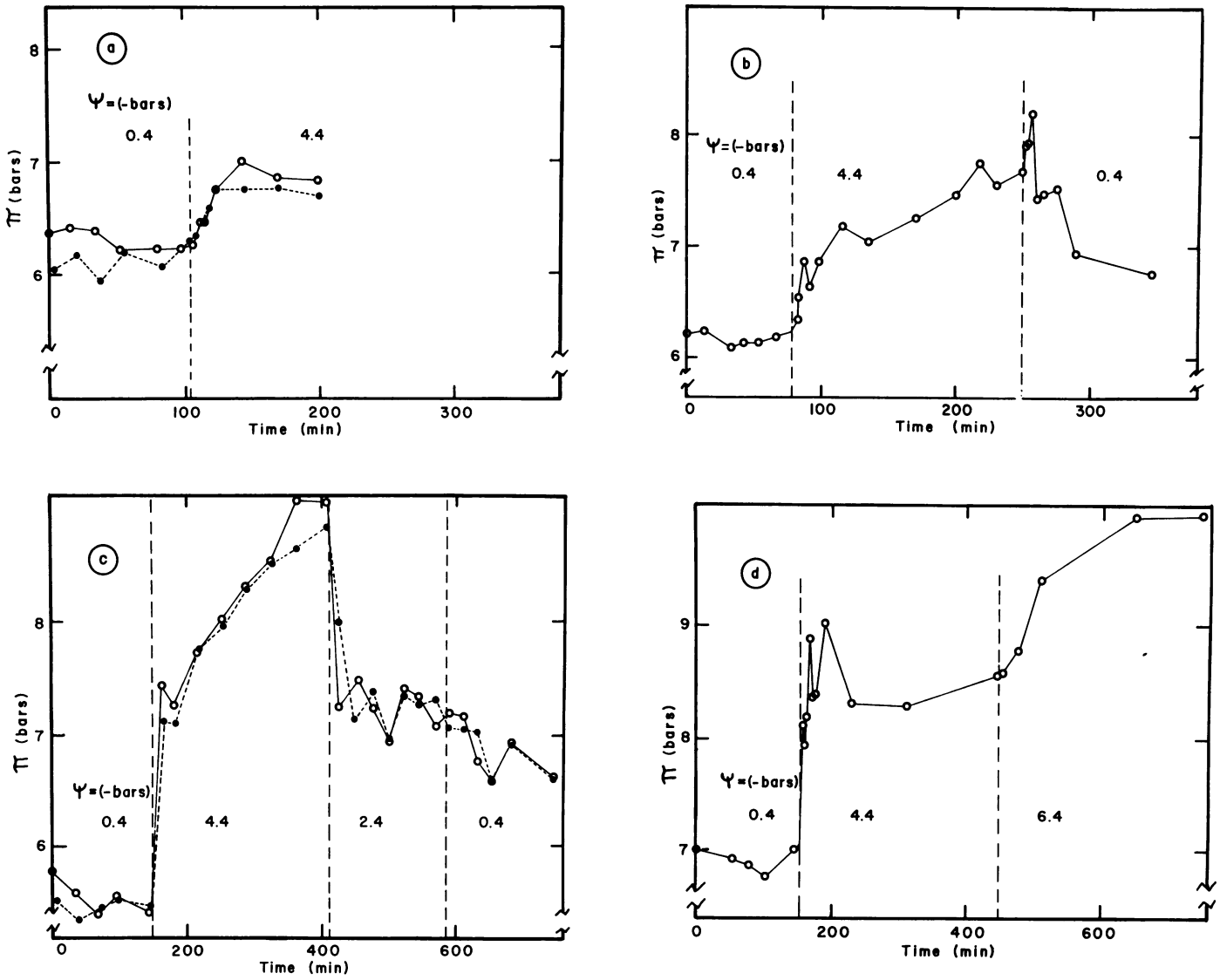

FIG. 3. Kinetics of the sieve tube π response to step changes in Ψ. Osmotic pressures were determined from freezing point measurements on stylet exudate collected for 15 to 30 s just before the sampling time. In two experiments (a and c), samples were collected from two stylets on the same bark strip.

segments. We, too, have consistently observed the latter type of response when stem segments were used instead of bark strips (unpublished observations). It seems possible that, if turgor regulation is occurring, the source of stored solutes may be mostly in the xylem ray parenchyma, the reserves of which are unavailable when bark strips are used. In the same experiments, we did not find a rapid π response to a $\Delta\Psi$, suggesting a substantially higher ϵ for sieve tubes in intact willow stems, perhaps because of a reinforcing effect by the intact bark. Observations on the kinetics of the turgor response in the sieve tubes of stem segments should allow a more confident evaluation of these points.

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