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Direct and Indirect Measurements of Phloem Turgor Pressure in White Ash

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ABSTRACT

Direct determinations and indirect calculations of phloem turgor pressure were compared in white ash (*Fraxinus americana* L.). Direct measurements of trunk phloem turgor were made using a modified Hammel-type phloem needle connected to a pressure transducer. Turgor at the site of the direct measurements was calculated from the osmotic potential of the phloem sap and from the water potential of the xylem. It was assumed that the water potentials of the phloem and xylem were close to equilibrium at any one trunk location, at least under certain conditions. The water potential of the xylem was determined from the osmotic potential of xylem sap and from the xylem tension of previously bagged leaves, measured with a pressure chamber. The xylem tension of bagged leaves on a branch adjacent to the site of the direct measurements was considered equivalent to the xylem tension of the trunk at that point. While both the direct and indirect measurements of phloem turgor showed clear diurnal changes, the directly measured pressures were consistently lower than the calculated values. It is not clear at present whether the discrepancy between the two values lies primarily in the calculated or in the measured pressures, and thus, the results from both methods as described here must be regarded as estimates of true phloem turgor.

A knowledge of the turgor pressure gradients which exist in the sieve elements of higher plants is essential to any evaluation of the pressure flow mechanism of phloem translocation. This mechanism, first proposed by Münch in 1930 (14), states that phloem transport consists of a mass flow of solutes and water, driven by an osmotically generated pressure gradient in the sieve elements. A number of attempts have been made to determine whether the pressure gradients found in the sieve elements are of sufficient magnitude to drive mass flow (5, 7, 8, 10, 15–17, 19). In these studies, two methods have been utilized to evaluate sieve-tube turgor and its gradient. (a) Turgor pressure can be calculated from other parameters of the system, specifically, water potential of the phloem and osmotic potential of the sieve-tube sap (5, 8, 10, 15). (b) Turgor pressure can be measured directly (1, 2, 7, 16, 17, 19).

Kaufmann and Kramer in 1967 (10) found no evidence of a turgor gradient in the presumed direction of transport in the phloem of red maple. Using thermocouple psychrometers, these workers measured ψ[3] of phloem discs removed from the upper and lower parts of the trunk; following feeezing and thawing of the samples, ψ_π of the same discs was determined. Since an ψ_π measured in this manner is an average for the entire phloem, it is likely that turgor pressures calculated from these values reflect an average phloem turgor, rather than turgor in the sieve elements alone. Rogers and Peel (15) repeated these experiments in 1975, using small willow trees and cuttings. While ψ of the phloem was measured in the same way as in the previous study, ψ_π was determined from sieve-tube sap, collected either from severed aphid stylets or from incisions made in the phloem. Turgor calculated from these measurements is more likely to estimate sieve-tube turgor specifically. Using this refined technique, Rogers and Peel demonstrated that calculated sieve-tube turgor is higher at the apex than at the base of willow stems; turgor gradients lay between 0.5 and 2.7 atm m^{-1}. Housley and Fisher (8) and Fisher (5) also calculated sieve-tube turgor in their studies of soybean. Source leaf ψ was determined by a psychrometric method, while root (sink) ψ was estimated on the basis of leaf and nutrient solution ψ values. Assuming that all of the solute in the sieve tubes was in the form of sucrose, these workers calculated the ψ_π of the sieve-tube sap from the sucrose concentration, measured either by quantitative microautoradiography (8) or by a negative staining procedure (5). Using the latter, more reliable technique, Fisher (5) calculated pressure differences between source and sink of approximately 4.1 bars. Since transport velocities and sieve-tube dimensions were also measured, pressure differences required to drive mass flow in these plants could be estimated. These differences range from 1.2 to 4.6 bars and thus compare favorably with the calculated pressure differences.

Turgor pressures calculated from sieve element ψ and ψ_π are subject to any errors or assumptions inherent in measuring these two parameters. For this reason, a number of investigators have preferred direct measurements of turgor pressure to calculated values. A recent review (23) discusses direct measurements in systems other than the phloem, in particular, algal systems. With regard to the phloem, the majority of workers favored manometric determinations of sieve-tube turgor (1, 2, 7, 16, 17, 19). In the earliest studies conducted on laticiferous phloem tissues (1, 2), the "turgor pressures observed probably derive mainly from the latex vessels and do not necessarily reflect conditions within the translocatory system" (2). However, various observations made in the course of these studies indicate the potential accuracy of manometric techniques; these include a positive correlation with atmospheric RH, negative correlations with changes in temperature, transpiration, leaf water deficit, and stomatal opening, and finally the lack of such correlations in leafless trees. Hammel (7) applied essentially the same methods to a study of turgor pressure and its gradient in the phloem of red oak; he reported wide variations in measured pressures at any given height in the tree. On the average, however, turgor pressures measured 6.5 m up the trunk were 0 to 3 atm higher than those at 1.5 m, thus favoring the pressure flow hypothesis. The phloem-needle manometric device developed by Hammel has been used with herbaceous

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[3] Abbreviations: ψ, water potential; ψ_π, osmotic potential; ψ_P, turgor pressure.

plants as well as with trees. Sheikholeslam and Currier (16, 17) studied pressure gradients in *Ecballium elaterium* and reported that there is a direct correlation between the direction of assimilate transport and the pressure difference between two different heights on the stem.

In general, the available data tend to support the concept of an osmotically generated mass flow in the phloem. The validity of this conclusion is based on the accuracy of the techniques employed to estimate phloem turgor pressure. Both calculated and directly measured pressures are open to question, due to a variety of difficulties inherent in the techniques themselves. The present study sought to compare data obtained by both methods in order to evaluate the accuracy with which these techniques estimate phloem turgor pressures.

MATERIALS AND METHODS

Plant Material. Four mature white ash trees (*Fraxinus americana* L.) at Harvard Forest, Petersham, MA, were utilized for these studies. Tree size ranged from 22.5 to 47 cm diameter at breast height.

Experimental Procedure and Calculations. The methods used in this study are similar to those developed in the past for direct measurement and calculation of phloem turgor in tree trunks. However, pressures were measured with a pressure transducer, rather than with a manometer, connected to a Hammel-type phloem needle (7). The transducer has the advantage of a linear response to pressure, as well as requiring a small amount of sap flow (approximately 2.6 μl) for full scale response. Calculated values were also derived in a somewhat different manner. The overall ψ of the xylem, rather than that of the phloem, was measured. Turgor was calculated from the xylem ψ and phloem-sap ψ_π, with the assumption that the ψ values of phloem and xylem were in equilibrium at any one given location, at least at night when flow rates in the xylem are low.

At each sampling time, three measurements were made: direct phloem-pressure measurement, osmotic potential of the phloem sap, and xylem pressure potential or tension. The phloem turgor measured directly was compared with the turgor calculated from the following equations:

$$\psi_{\text{phloem}} = \psi_{\text{xylem}}$$

$$\psi_{P[\text{phloem}]} + \psi_{\pi[\text{phloem}]} = \psi_{P[\text{xylem}]} + \psi_{\pi[\text{xylem}]}$$

$$\psi_{P[\text{phloem}]} = (\psi_{P[\text{xylem}]} + \psi_{\pi[\text{xylem}]}) - \psi_{\pi[\text{phloem}]}$$

Direct Turgor Measurement. A modified Hammel-type phloem needle was used (Fig. 1). The needles were constructed from 23-gauge hypodermic needles, joined to high pressure plastic tubing (3 mm o.d., 1.5 mm i.d.) with a plastic tubing adapter (Clay Adams, tubing to male Luer-lock adapter). At the opposite end, the tubing was joined with a specially machined fitting to a bonded strain gauge pressure tranducer (model 540, 0–250 p.s.i. or 0–500 p.s.i., MBIS, Inc., Bedford Heights, OH), and the entire apparatus was filled with mineral oil. A 10 v input to the transducer was supplied by a regulated low voltage power supply (Heathkit model IP-28) and the output (0 to approximately 30 mv) was recorded with a strip-chart recorder (Heath-Schlumberger model SR-204). Following removal of the rough portion of the cork from the trunk, readings were made by inserting the needle into the bark down to the wood. This position was indicated by a much higher resistance to needle movement.

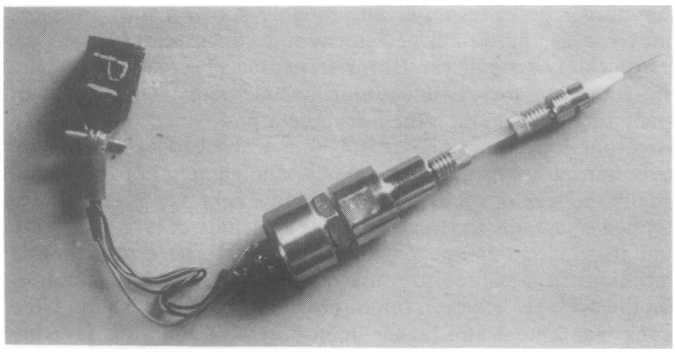


FIG. 1. Pressure transducer apparatus.

A pressure reading was considered acceptable if it met the following criteria:

1. There was no visible indication of external leakage of phloem sap.
2. Once the needle had reached the innermost phloem layer, an immediate, rapid, and smooth rise in the pressure reading occurred. Removal of the needle resulted in an immediate decrease to zero. Both responses are indicative of an unblocked phloem needle.
3. The reading persisted for a reasonable period of time. Two trees showed very rapid rises in the transducer output and reached higher pressures than the other trees. In these cases, readings which fell before 0.5 min were rejected. For the remaining two trees, the limit was set at 1 min.

Measurement of Phloem-Sap Osmotic Potential. Samples of phloem sap (approximately 30 μl) were collected in capillary tubes directly from the puncture made by the phloem needle, following removal of the needle. ψ_π of the sap was measured using a dew point microvoltmeter (Wescor, Logan, UT) equipped with an appropriate sample chamber (Wescor C-52 sample chamber). The psychrometer was calibrated periodically with NaCl samples and was used in the dew point mode of operation, as described in the Wescor manual.

Measurement of Xylem Tension. Each of the trees selected had a lowermost branch which was reasonably accessible, with few other branches at the same level. All of the leaves on the lowermost branch that were later used for measurement were individually bagged using small plastic bags with twist ties. The remaining leaves were removed from the branch to prevent transpiration. This bagging procedure was generally carried out the afternoon or evening preceding the beginning of experimentation, in order to allow the xylem tension in the branch to come into equilibrium with the xylem tension in the tree trunk. In some cases, pressure potential of unbagged leaves from a second branch was also determined for comparison with data from bagged leaves. The xylem tension was measured with a Scholander-type pressure chamber.

Measurement of Xylem Osmotic Potential. Xylem sap was occasionally collected by applying pressures in excess of the balancing pressure to the leaves in the pressure chamber and gathering sap (5 μl) from the cut petioles. ψ_π of the xylem sap was measured in the same way as described for phloem sap. There was little variation in the values obtained and no clear pattern with regard to time of day. The average of 13 values from four trees was 1.2 ± 0.2 bars; this average value was used for $\psi_{\pi[\text{xylem}]}$ in the calculations described above.

RESULTS

Measurement of Xylem Tension. It has been suggested that the ψ of a leaf brought into vapor pressure equilibrium with a small enclosed space will reflect the ψ of the stem xylem (11, 21). For this reason, the xylem pressure potential was estimated with a Scholander-type pressure chamber using previously bagged leaves of white ash. Unbagged leaves were also measured for comparison with data from bagged leaves. Figure 2 illustrates the differences in tension between bagged and unbagged leaves taken from the same tree at various times of day and measured simultaneously.

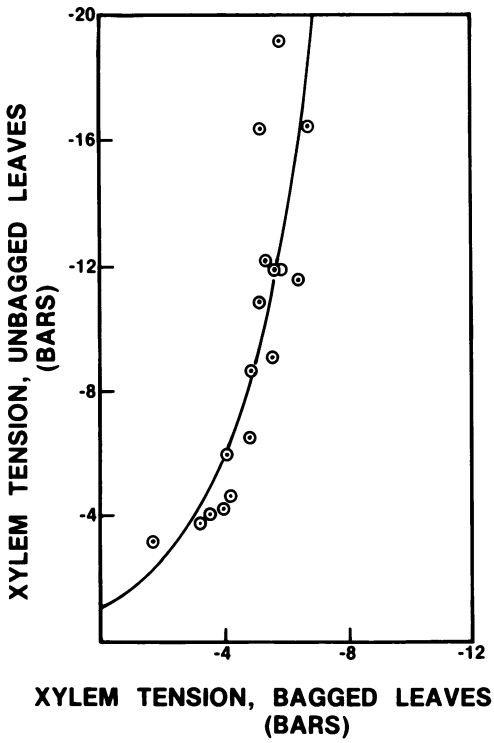


FIG. 2. Relationship between xylem tensions in bagged and unbagged leaves. Each point represents one determination of both bagged and unbagged leaves from the same tree at the same time. Unbagged leaves were taken from a branch adjacent to that on which the leaves were bagged. The range of values reflect the diurnal march of xylem tensions. The solid line is the best fit line ($Y = 1.11\ e^{0.41X}$, $n = 17$, $r = 0.89$).

The values for bagged leaves are more positive than for unbagged leaves whenever the xylem tension exceeds approximately −4 bars. In addition, differences between bagged and unbagged leaf measurements are largest when xylem sap velocities are presumably the highest, *i.e.* at midday, and decrease as sap velocities decrease during the afternoon hours (data not shown). These results support the concept that xylem tensions of bagged leaves estimate values in the trunk, while unbagged leaf values reflect conditions in the leaves themselves. It is likely that the differences between the two values are a result of the gradient of ψ from trunk to leaf xylem, driving transpirational flow. It is also true, however, that the bagged leaf values may not coincide with the xylem tensions existing in the trunk at precisely the point where the phloem-pressure measurements were made. For a discussion of these problems, see Zimmermann (22).

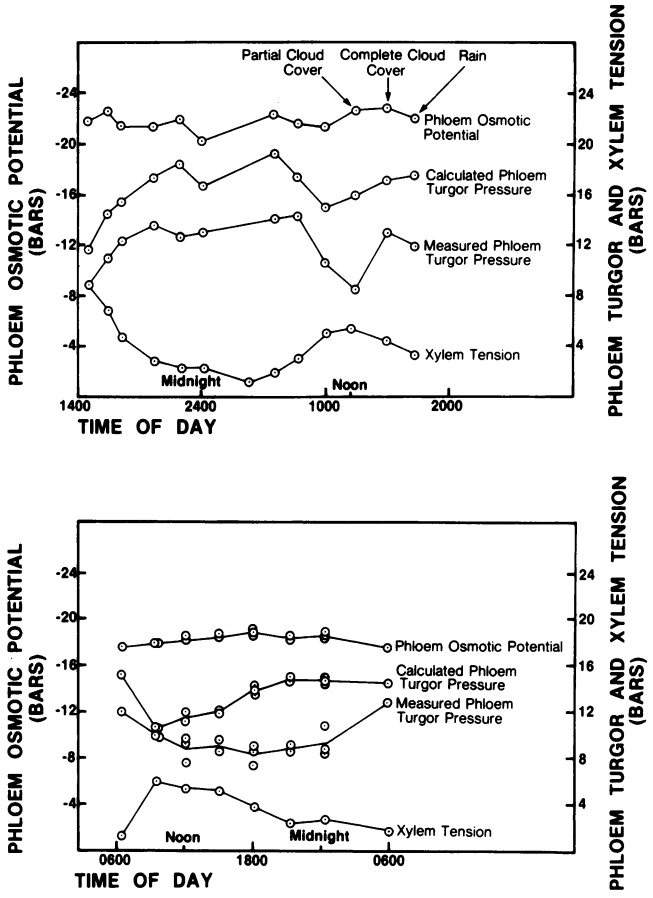
Measurement of Phloem Turgor Pressure. Following insertion of the phloem needle, measurements rose quickly to a maximum value, as long as the needle was not blocked by debris or coagulated sap from previous readings. Leakage around the needle, both external and presumably internal as well, resulted in extremely short lived responses, which decreased rapidly. To eliminate those readings which were obviously in error due to leakage, the criteria for acceptable measurements were established. Even so-called acceptable readings decreased from the maximum level before the needle was removed from the bark. However, two or more acceptable turgor-pressure measurements made consecutively and in close proximity on the tree trunk were generally quite similar, as shown in Table I. The average difference between two such measurements was 1.1 bars, with the difference ranging from 0 to a maximum of 5.9 bars. Turgor pressures calculated at the same time are also shown in Table I.

Changes in calculated and measured phloem turgor pressures were followed over a 24-h period for two of the trees studied (Figs. 3 and 4). In general, both measured and calculated phloem turgor reach a minimum at midday, when xylem tensions are highest, and a maximum in the early morning hours, when the xylem is in its most relaxed state. This pattern is expected to result from exchange of water between phloem and xylem (10). While the two values for turgor follow similar diurnal patterns, the measured turgor seems to lag behind the calculated pressure (Fig. 3 in particular), with measured pressures reaching a maximum or minimum 2 to 4 h after the calculated ones. Xylem tensions in these graphs show a typical diurnal response, while little or no pattern with time is detectable for phloem ψ_π. Any diurnal pattern

Table I. *Calculated and Measured Turgor Pressures in White Ash*

Measured pressures recorded for the same time of day were determined within 35 min of each other and within 2–3 cm on the trunk, with the exception of tree 4. For tree 4, readings were taken at three equidistant points on the trunk (approximately 50 cm apart). Refer to text for general experimental methods.

Tree	Approximate Time of Day	Measured Pressure	Calculated Pressure
		bars	
1	1715	11.0	14.5
		12.4	15.4
	2000	14.1	18.1
		13.0	16.7
	1600	12.0	11.6
		12.1	11.8
2	1230	7.3	11.7
		8.9	12.2
	1500	9.5	13.4
		8.5	13.5
	1815	9.2	14.6
		8.6	16.1
	1300	9.2	10.6
		7.9	10.7
3	1215	7.3	10.2
		8.1	8.6
	1630	10.2	11.9
		8.8	12.0
	1930	9.5	12.8
		9.8	13.4
	0915	10.1	10.6
		10.1	10.6
	1145	9.2	11.8
		7.6	11.5
		9.6	11.3
	1500	9.5	11.9
		8.6	12.1
	1815	9.0	13.6
		7.3	13.8
		8.5	14.2
	2115	9.1	15.0
		8.6	14.6
	0015	8.7	14.7
		10.8	14.6
		8.5	14.9
4	0600	11.4	20.6
		12.2	19.6
	0900	13.9	15.2
		12.8	16.5
		13.5	15.2
	1500	13.2	17.6
		12.5	17.6
		12.6	17.9
	0200	17.3	22.2
		11.4	21.9



FIGS. 3 and 4. Diurnal cycles of calculated and measured phloem turgor, xylem tension, and phloem osmotic potential. Each phloem osmotic potential is an average of two measurements made on phloem sap collected from a single puncture; the two values used for averaging are all within 1 bar of each other. Each xylem tension is an average of two determinations made using separate leaves; the two values are within 1 bar of each other, with approximately 80% of the two averaged values being within 0.5 bar of each other. Measured turgor pressures represent single determinations, while calculated pressures are derived from the osmotic potential of sap from a single phloem needle puncture (average of two values), the xylem tension at that time of day (average of two values), and the average xylem osmotic potential (−1.2 bars). Figure 3, tree 1; Figure 4, tree 3.

in solute content of the sap is apparently masked by changes due to sampling different areas on the trunk over the 24-h period.

The diurnal curves (Figs. 3 and 4) clearly demonstrate, in addition, that the measured phloem turgor pressures were always lower than the calculated values. This is also indicated in Figure 5, where all measured pressures are plotted as a function of the turgor calculated at the same time. In general, the higher the calculated pressure, the greater is the discrepancy between calculated and measured values. No readings were obtained between 0 and 7 bars, where the two measurements might have approached equality.

DISCUSSION

Phloem turgor pressures, both calculated and measured, show clear diurnal changes in white ash, presumably as a result of diurnal changes in xylem tensions and ensuing water flux between the two systems. However, a discrepancy exists between the values for turgor obtained by the two methods utilized, with measured pressures falling below the calculated values. Two possible explanations exist for this discrepancy: either the phloem-needle technique fails to measure sieve-tube turgor adequately, or an error was made in choosing parameters to measure for calculating turgor.

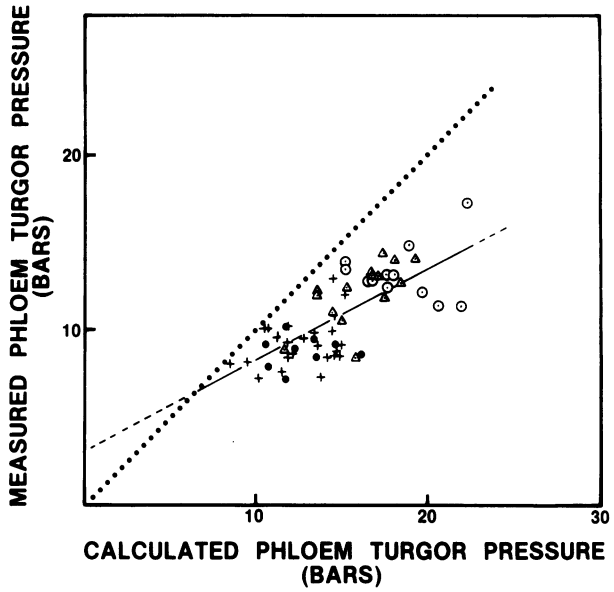


FIG. 5. Measured phloem turgor pressures as a function of pressures calculated at the same time. Number of determinations and ranges are the same as in Figures 3 and 4. The dotted line represents equality between the two values, while the solid line is the best fit line ($Y = 0.52\ X + 3.05$, $n = 61$, $r = 0.71$). △, tree 1; ●, tree 2; +, tree 3; ○, tree 4.

In terms of calculated pressures, the most obvious possible sources of error are the assumptions made regarding the measurement of ψ. As discussed previously, the ψ of bagged leaves was regarded as equivalent to trunk ψ, although it is not certain if the value measured is accurate for the exact point of pressure measurement. An error here would almost certainly result in a xylem ψ that is too negative and thus in a lower calculated pressure, *i.e.* one closer to the measured value. Direct measurements of xylem ψ in the trunk and of gradients from trunk to leaf are necessary to any further understanding of this problem. Of more importance is the assumption that the ψ values of phloem and xylem in the trunk are in equilibrium. It has generally been assumed that water movement can occur freely between the phloem and xylem (2, 10). Such an assumption is supported, at least for small woody plants, by studies on changes in phloem-sap concentration and rates of exudation in response to changes in xylem ψ or tension (6, 18); furthermore, measurements of xylem tension and concomitant changes in phloem hydration indicate that there is a close association of phloem and xylem in terms of radial water movement (13). However, even if there is a free flux of water between the two tissues, the ψ values of phloem and xylem are probably not in exact equilibrium during daylight hours, when incoming radiation is high and xylem sap velocities are rapid. In addition, xylem ψ is in a state of flux during the day, due to changing transpirational demand. Under these conditions, a time lag between calculated and measured phloem pressures is likely, due to a lag in equilibration between xylem and phloem ψ values. However, at night or on heavily overcast days, the measured pressures should approach the calculated ones, or at least the predicted lag should be shortened during those times when xylem tension is low and not changing greatly. The concept of a lag between xylem tensions and phloem responses in tree species has been given some support by studies on the relationship between leaf ψ and stem diameter in Douglas fir (12, 20); changes in stem diameter, due largely to changes in phloem hydration, were reported to be out of phase with leaf ψ by several hours. In white ash, diurnal curves of

calculated and measured pressures also show a lag period, when the timing of maximum and minimum turgor is considered (Fig. 3). This lag may reflect the delay in equilibration of phloem ψ with xylem ψ. In addition, it appears that the measured pressure slowly approaches the calculated turgor from 1800 to 0600 h in tree 3 (Fig. 4), further supporting this concept.

Thus, without compelling evidence to the contrary, the assumptions made with reference to calculated turgor seem warranted. At the same time, however, it is clear that measured pressures never reach the calculated values in white ash. At least two problems with the phloem-needle technique must be considered. The size of the needle used is massive in comparison with the size of the sieve elements, and a large number of cells are destroyed when the needle is inserted. Figure 6 shows a transverse section of the tissues involved in these measurements as well as a typical phloem needle, both at the same magnification. In this particular case, the phloem layer is consistently five sieve elements thick, with 19 such rows equalling the width of the phloem needle. Thus, approximately 95 sieve elements would be broken when the needle is inserted, illustrating the large number of cells disrupted during the pressure measurements. Even though readings were rejected whenever a visible external leakage of sap occurred, the possibility cannot be ruled out that an internal leakage of sap into intercellular spaces occurred, reducing the measured pressure. The fact that almost all readings decreased after reaching a maximum value and before the needle was extracted from the bark lends credence to this possibility. In addition, white ash exudes sap quite freely over relatively extended periods of time; the initial burst of exudation due to pressure release may compound the problem of internal leakage.

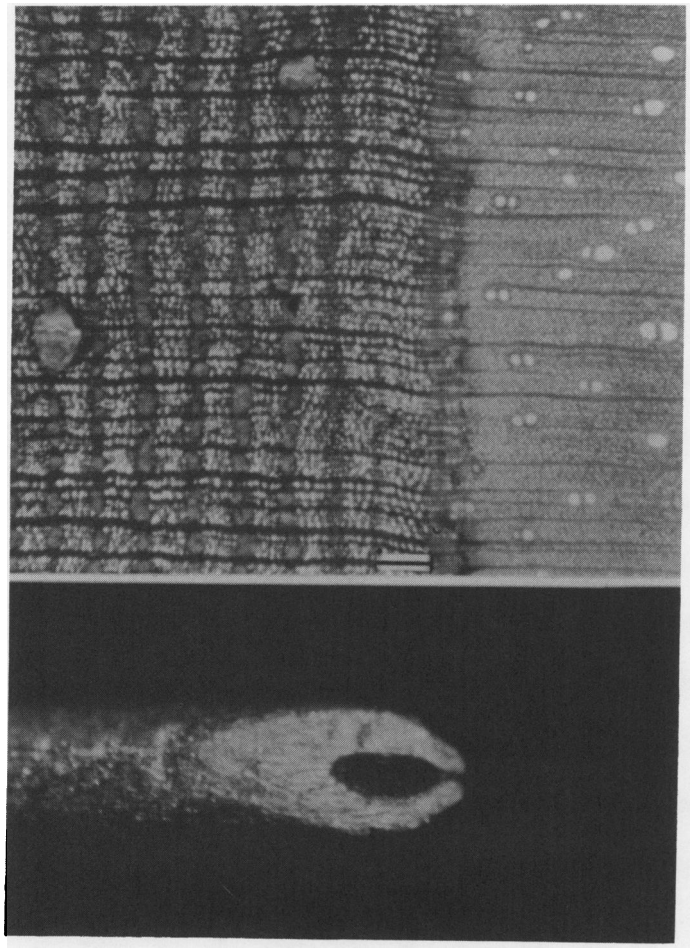


FIG. 6. Transverse section of the innermost phloem, cambium, and outermost xylem of a trunk of white ash and a typical phloem needle used to directly measure phloem turgor. Both the tissue section and the phloem needle are at the same magnification (approximately × 25). The bar on the tissue section represents the width of the conducting phloem, approximately 0.30 mm.

Furthermore, the fact that detection of pressure requires sap flow into the phloem needle implies that measurement of turgor decreases the turgor itself due to shrinkage of the sieve elements. The extent to which pressure is reduced depends on the change in cell volume and on ϵ, the volumetric elastic coefficient of the cell wall, according to the following equation:

$$dP = \epsilon\, dV/V \quad (3)$$

where P represents turgor pressure and V is cell volume. In addition, the pressure decrease due to shrinkage of the sieve elements may be compounded by volume changes due to compressibility of the apparatus (9). ϵ values of 2 to 25 bars have been reported for cells in higher plant tissues (4, 9). Since no information is available on the shrinkage of sieve elements during pressure measurements using the phloem needle, a quantitative evaluation of the pressure drop cannot be made. However, consideration of the sap flow required to establish pressure readings of the magnitude recorded for white ash indicates that this effect could be considerable even when a pressure transducer is utilized which requires only a few μl of sap flow for full range pressure detection. For example, in the tissue illustrated in Figure 6, the volume of sap required to obtain a full scale reading with the pressure transducer corresponds to the volume of the sieve elements 2.8 cm on either side of the needle puncture. In reality, of course, the sieve elements are never fully collapsed, and sap flow must occur from areas considerably more distant than several centimeters. A full scale reading corresponds to a pressure of 17.3 bars, the maximum value recorded in this study. Both the effect of internal leakage and of pressure loss due to volume changes should increase with increasing pressure, as has been noted (Fig. 5). The maximum pressure that can be recorded in white ash may depend on a balance between the response time of the pressure detecting apparatus and the time required for leakage to become appreciable, as well as on the magnitude of pressure loss due to shrinkage of the sieve elements.

At present, the possibility of measuring pressure gradients in white ash and the question of the technique preferred must be approached with caution. The wide variation in recorded pressures at the same height on the trunk noted in Hammel's data on red oak (7) points to the same necessity, no matter which species is studied. More information is required to determine whether the differences between calculated and measured turgor reported here for white ash are due primarily to inaccurate assumptions with regard to phloem ψ or to the phloem-needle technique. Studies are currently being conducted to evaluate the errors involved in the methods utilized in this study. A direct measurement of phloem ψ is being investigated; in addition, red oak, which exudes less freely than white ash, is being studied in order to minimize difficulties due to leakage and pressure loss. Further research on sieve-element turgor should also investigate the use of the pressure probe described by Hüsken *et al.* (9), which compensates for volume changes in the system during the course of pressure measurements. Until these problems are resolved, both directly measured and calculated phloem pressures as described here must be regarded as estimates of true phloem turgor.

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LITERATURE CITED

1. BUTTERY BR, SG BOATMAN 1964 Turgor pressures in phloem: measurements on *Hevea* latex. Science 145: 285–286
2. BUTTERY BR, SG BOATMAN 1966 Manometric measurement of turgor pressures

in laticiferous phloem tissues. J Exp Bot 10: 1–16
3. DAINTY J 1976 Water relations of plant cells. *In* U Lüttge, MG Pitman, eds, Encyclopedia of Plant Physiology, New Series, Vol 2, Part A. Springer-Verlag, Berlin, pp 12–35
4. FERRIER JM, J DAINTY 1977 A new method for measurement of hydraulic conductivity and elastic coefficients in higher plant cells using an external force. Can J Bot 55: 858–866
5. FISHER DB 1978 An evaluation of the Münch hypothesis for phloem transport in soybean. Planta 139: 25–28
6. HALL S, JA MILBURN 1973 Phloem transport in *Ricinus*: its dependence on the water balance of the tissues. Planta 109: 1–10
7. HAMMEL HT 1968 Measurement of turgor pressure and its gradient in the phloem of oak. Plant Physiol 43: 1042–1048
8. HOUSLEY TL, DB FISHER 1977 Estimation of osmotic gradients in soybean sieve tubes by quantitative autoradiography. Qualified support for the Münch hypothesis. Plant Physiol 59: 701–706
9. HÜSKEN D, E STEUDLE, U ZIMMERMANN 1978 Pressure probe technique for measuring water relations of cells in higher plants. Plant Physiol 61: 158–163
10. KAUFMANN MR, PJ KRAMER 1967 Phloem water relations and translocation. Plant Physiol 42: 191–194
11. LANG ARG, HD BARRS 1965 An apparatus for measuring water potentials in the xylem of intact plants. Aust J Biol Sci 18: 487–497
12. LASSOIE JP 1973 Diurnal dimensional fluctuations in a Douglas-fir stem in response to tree water status. Forest Sci 19: 252–255
13. MOLZ FJ, B KLEPPER, VD BROWNING 1973 Radial diffusion of free energy in stem phloem: an experimental study. Agron J 65: 219–222
14. MÜNCH E 1930 Die Stoffbewegungen in der Pflanze. Gustav Fischer, Jena
15. ROGERS S, AJ PEEL 1975 Some evidence for the existence of turgor pressure gradients in the sieve tubes of willow. Planta 126: 259–267
16. SHEIKHOLESLAM SN, HB CURRIER 1977 Phloem pressure differences and ^{14}C-assimilate translocation in *Ecballium elaterium*. Plant Physiol 59: 376–380
17. SHEIKHOLESLAM SN, HB CURRIER 1977 Effect of water stress on turgor differences and ^{14}C-assimilate movement in phloem of *Ecballium elaterium*. Plant Physiol 59: 381–383
18. WEATHERLEY PE, AJ PEEL, GP HILL 1959 The physiology of the sieve tube. Preliminary experiments using aphid mouth parts. J Exp Bot 10: 1–16
19. WRIGHT JP, DB FISHER 1980 Direct measurement of sieve tube turgor pressure using severed aphid stylets. Plant Physiol 65: 1133–1135
20. ZAERR JB 1971 Moisture stress and stem diameter in young Douglas-fir. Forest Sci 17: 466–469
21. ZIMMERMANN MH 1971 Transport in the xylem. *In* MH Zimmermann, CL Brown, Trees: Structure and Function, Chap. 4. Springer-Verlag, New York, pp 169–220
22. ZIMMERMANN MH 1978 Hydraulic architecture of some diffuse-porous trees. Can J Bot 56: 2286–2295
23. ZIMMERMANN U 1978 Physics of turgor- and osmoregulation. Annu Rev Plant Physiol 29: 121–148