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# CANNY'S COMPENSATING PRESSURE THEORY FAILS A TEST[1]

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Canny's compensating pressure theory for water transport (*American Journal of Botany* 85: 897–909) has evolved from the premise that cavitation pressures are only a few tenths of a megapascal negative (approximately −0.3 MPa). In contradiction, ''vulnerability curves'' indicate that xylem pressures can drop below −3 MPa in some species without causing a loss of hydraulic conductivity. Canny claims these curves do not measure the limits to negative pressure by cavitation, but rather the limits to the compensating tissue pressure that otherwise quickly refills cavitated conduits. Compensating pressure is derived from the turgor pressure of the living cells in the tissue. To test this claim, we compared vulnerability curves of *Betula nigra* stems given three treatments: (1) living control, (2) killed in a microwave oven, and (3) perfused with a −1.5 MPa (10% w/w) mannitol solution. According to Canny's theory, the microwaved and mannitol curves should show cavitation and loss of conductance beginning at approximately −0.3 MPa because in both cases, the turgor pressure would be eliminated or substantially reduced compared to controls. We also tested the refilling capability of nonstressed stems where compensating pressure would be in full operation and compared this with dead stems with no compensating pressure. According to Canny's interpretation of vulnerability curves, the living stems should refill within 5 min. Results failed to support the compensating tissue theory because (a) all vulnerability curves were identical, reaching a −1.5 MPa threshold before substantial loss of conductance occurred, and (b) killed or living stems had equally slow refilling rates showing no significant increase in conductivity after 30 min. In consequence, the cohesion theory remains the most parsimonious explanation of xylem sap ascent in plants.

**Key words:** cavitation; cohesion theory; compensating pressure theory; embolism; water transport.

Martin Canny has been very successful in promoting his compensating pressure theory for plant water transport. In addition to an article in the *American Scientist* (Canny, 1998b), the *American Journal of Botany* recently featured the theory as a ''Special Invited Paper'' (Canny, 1998a). At the heart of his theory is that pressures below approximately −0.3 MPa do not exist in xylem because of cavitation. These modestly negative pressures are maintained by compression of the water column by surrounding turgid tissue. This compensating tissue pressure not only minimizes the negative pressures necessary for transport, but quickly refills any cavitated and embolized conduits by squeezing water from the cells to fill up the empty conduits. The result is a ''self-sustaining, ultrastable pathway'' (Canny, 1998a).

To develop a new water transport theory and to have it be accommodated so enthusiastically, there must be significant problems with our understanding of water transport in plants as represented in the cohesion theory of the textbooks. Of course, what has dogged the cohesion theory from the outset is its prediction of substantial negative pressures. These pressures are required to extract water from dry or saline substrates, move it against the frictional resistance of soil and plant, and against gravity. Water pressures down to −10 MPa or lower have been claimed in the xylem of plants. These pressures are far below the vapor pressure of water, and therefore highly metastable. Disbelief of these low negative pressures is the motivation for alternative explanations.

The deciding point in the cohesion vs. compensation debate is therefore the evidence for the existence of substantial negative pressures in xylem. We will not repeat extensive discussions of the evidence for the cohesion theory (Tyree, 1997), and critiques of xylem pressure probe experiments of U. Zimmermann and colleagues (Zimmermann et al., 1994) that claim to show a negative pressure limit of approximately −0.4 MPa in the xylem (Steudle, 1995; Sperry et al., 1996; Tyree, 1997). We will not indulge in exposing internal flaws in Canny's theory, although this is a useful exercise (see Comstock, this issue). What we will do is focus on the validity of what we feel is the most direct test of the negative pressure limit in intact xylem conduits of plant xylem.

This test is a natural extension of Brigg's classic experiment using centrifugal force to demonstrate cavitation pressures below −25 MPa in water-filled capillary tubes (Briggs, 1950). The test consists of replacing the capillary tube with a stem segment (Holbrook, Burns, and Field, 1995; Pockman, Sperry, and O'Leary, 1995). The results show that the negative pressure generated in this manner matches pressure chamber measurements and that negative pressures below −3 MPa can exist without cavitation. The cavitation pressure was inferred from ''vulnerability curves'' that show the relationship between negative xylem pressure and the loss of conductivity (Fig. 1). It is assumed that the cause of this loss of conductivity is the gas blockage of xylem conduits (''embolism'') that follows their cavitation (Pockman, Sperry, and O'Leary, 1995).

Unfortunately, these experiments have turned out to be consistent with Canny's theory as well (Canny, 1998a)! Canny interprets vulnerability curves as exposing the limits not to negative pressure, but to the compensating tissue pressure derived from the turgor pressure of the

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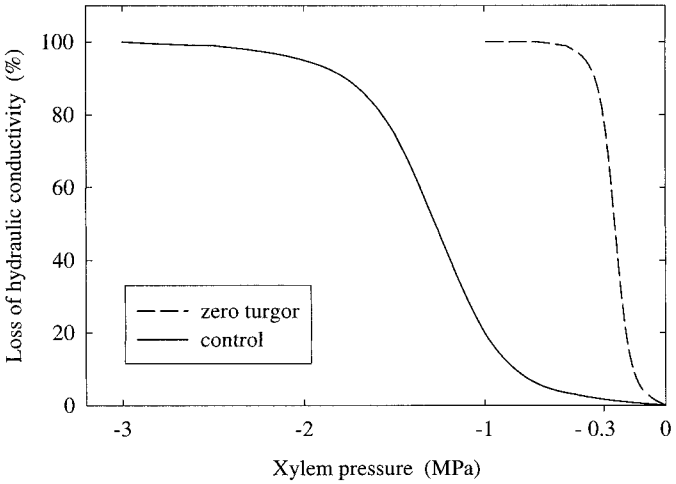


Fig. 1. Hypothetical vulnerability curves showing the loss of hydraulic conductivity with xylem pressure. The solid line is for living ''control'' stems showing a result typical of riparian tree species with a loss of conductivity initiated a few tenths of a megapascal below −1 MPa (Sperry and Saliendra, 1994; Pockman, Sperry, and O'Leary, 1995). The dashed line is the vulnerability curve predicted by the compensating pressure theory for stems in which turgor pressure has been eliminated. According to the theory, eliminating turgor pressure eliminates tissue pressure, which is responsible for refilling cavitated conduits. By eliminating the refilling process, the true cavitation pressure of approximately −0.3 MPa is revealed in the vulnerability curve.

living cells in the tissue. The compensating pressure is seen as refilling the vessels that actually cavitate at approximately −0.3 MPa, creating the illusion that cavitation has not occurred. Loss of conductivity is only seen when the cells have been exposed to sufficient stress to eliminate turgor pressure and, thus, their refilling activity. Canny's critique of the other methods we have employed for studying the cavitation process (Sperry and Saliendra, 1994) suggests that they, too, were in error.

Is Canny correct about the cavitation pressure in plants? To answer this question, we conducted simple experiments that tested the most fundamental predictions of the compensating pressure theory. Some of the experiments were suggested by Canny himself as crucial to settling the question (Canny, 1998a).

If Canny is right, vulnerability curves of killed or otherwise turgor-reduced stems will show a loss of conductivity near approximately −0.3 MPa because the turgor-powered refilling process would be eliminated (Fig. 1, dashed curve). The loss of conductivity in these curves would reflect the true cavitation pressure of the xylem. Living control stems would show a loss of conductivity at some lower negative pressure indicating the lower limit to the refilling activity of the living cells (Fig. 1, solid curve).

We also tested the relative refilling capability of control vs. killed stems where gas blockage was induced without stressing the tissue and thus eliminating its putative refilling capability. If Canny's interpretation of the vulnerability curve is correct, embolized conduits in living tissue must refill within the 5-min period between the induction of cavitation in the centrifuge and the subsequent conductivity measurement. The dead stems should refill much more slowly, if at all.

## MATERIALS AND METHODS

***Plant material***—One-year-old, bare-rooted seedlings of River Birch (*Betula nigra* L.) were obtained from the North Carolina Forest Service (Raleigh, North Carolina) and grown in 0.008-$m^3$ pots containing a commercial soil mixture (Fafard-Mix No 3-B, Conrad Fafard Inc., Agawam, Massachusetts). The plants were subsequently transferred to a greenhouse (Duke University, Durham, North Carolina) where they were grown under well-watered conditions for an additional 3 mo.

***Experimental treatments***—Three 142-mm long segments (3.5–6.0 mm diameter) were cut from the stems of each seedling under water. Each segment was subjected to a different treatment. A total of seven seedlings were used, giving a sample size of seven stems per treatment. Control stems were untreated. Killed stems were heated in a microwave oven (Panasonic NN-5369A, Matsuhita Electric Corp. of America, Franklin Park, Illinois) at medium power. They were heated in three 2-min intervals with 1-min breaks to promote even heat distribution. Temperatures reached at least 75°C inside the stems based on thermocouple measurements made after removal from the oven. The heat treatment was sufficient to eliminate respiration as measured by a gas exchange system (Fig. 2A). The gas exchange system has been described earlier (Saliendra, Sperry, and Comstock, 1995) and differed only in that a smaller chamber (volume 72 $cm^3$) was used to accommodate the stems. Respiration rates of killed stems remained zero after 3 and 6 h of soaking stems in water (Fig. 2A). We also made hand sections of the xylem and compared the appearance of the cytoplasm with control stems. In ''blind'' tests, we were able to distinguish the heated stems from controls based on the disorganization of the cytoplasm.

Mannitol stems were perfused with a 10% (w/w) solution of mannitol with an osmotic potential of −1.47 MPa as measured with psychrometers (Fig. 2B, dotted line; Plant Water Status Instruments, Guelph, Ontario, Canada). Mannitol was chosen because it is a nonpermeating solute and does not otherwise harm the tissue (Steudle, 1993). Stems were perfused for a minimum of 3 h at a head of ~5 KPa. This was sufficient to lower the water potential of the xylem tissue (measured with psychrometers) to within a few tenths of a megapascal of the solution water potential (Fig. 2B, solid line). During perfusion, stems were also immersed in a mannitol solution of the same strength. Microscopic observations of bark and leaf cells in the mannitol solution indicated that it did not cause obvious plasmolysis.

***Vulnerability curves***—After being treated, stems were used for vulnerability curve measurements. Vulnerability curves show the percentage loss of hydraulic conductivity caused by centrifugally induced negative pressure. Prior to the first conductivity measurement, the stems were flushed for at least 15 min with purified water with an ~50 kPa hydraulic pressure head to refill any embolized vessels already present. Killed stems were flushed after the heat treatment to remove all gas bubbles that might have been caused by localized boiling during heating. Mannitol stems were flushed with purified water prior to being perfused for 3 h with mannitol as described above.

The hydraulic conductivity of flushed stems was calculated from the flow rate of measuring solution through the stem divided by the pressure gradient driving the flow. Pressure was induced by an hydraulic head of ~5 kPa, and the flow rate was measured gravimetrically. To improve the accuracy of the measurement, the flow under zero hydraulic head was measured before and after the pressure-induced flow for each stem. Small zero-pressure flow rates can exist because of osmotic or capillary water uptake by tissue and leaks in the system. The zero-pressure flow rate was averaged and subtracted from the flow under pressure to obtain the net flow rate caused by the pressure. Net flow rate was used to calculate the conductivity. The measuring solution was filtered (0.2-μm retention), purified water for killed and control stems and a 10% w/w mannitol solution made from the same water for the mannitol stems. During the conductivity measurement, stems were covered with either

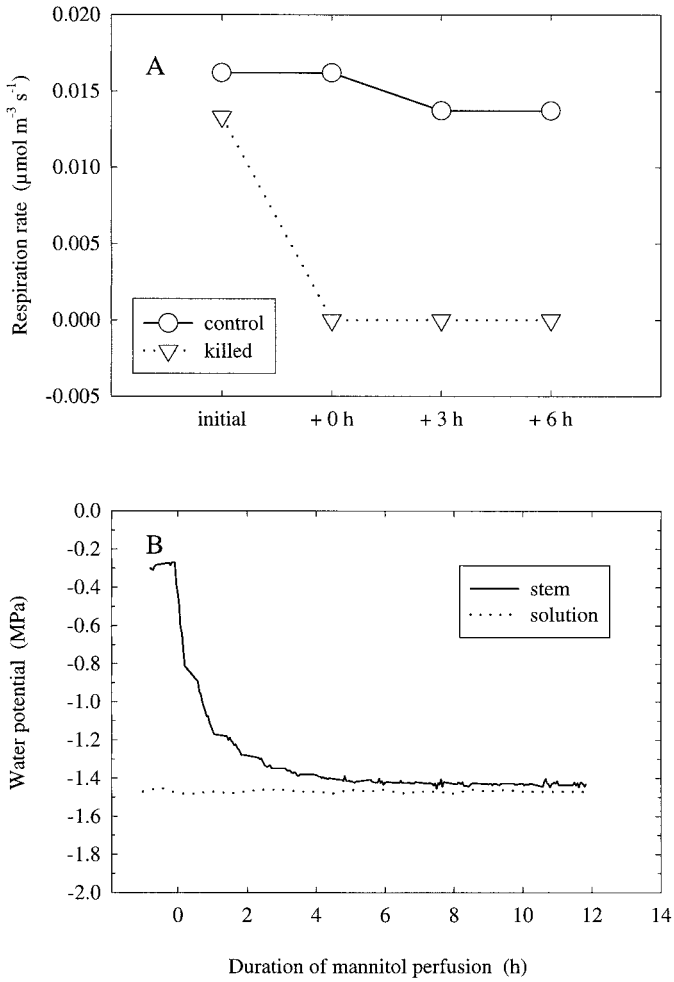


Fig. 2. (A) Respiration rates of control vs. killed stems measured at intervals following the microwave treatment for killed stems. Between respiration measurements, stems were soaked in water (as they were during conductivity measurements). Rates are based on pooled measurements of six stems. (B) Water potential of a 10% (w/w) mannitol solution (dotted line) and of a typical *Betula nigra* stem perfused with mannitol solution (solid line). Water potentials were measured with stem psychrometers.

water (control, killed) or mannitol solution (mannitol) to eliminate evaporation from the stems.

After the conductivity measurement, stems were spun for 4 min in a custom-built rotor designed to fit a Sorvall model RC5C centrifuge (Kendro Laboratory Products, Newton, Connecticut). In this way we could create precisely known negative pressures in the xylem water column (Pockman, Sperry, and O'Leary, 1995; Alder et al., 1997). After spinning, conductivity was measured and expressed as a percentage loss of the initial value. The stems were successively spun to increasingly lower pressures and remeasured until conductivity dropped > 95% from its initial value.

***Refilling experiments***—In a second experiment the refilling capability of six control and six killed stems was compared. Stems were flushed for 15 min with filtered and purified water at 50 kPa hydraulic pressure to refill embolized vessels. The conductivity was measured, stems were submerged in water, and air was injected at 0.1 MPa into the upstream end (with respect to the flow measurement) of the stems for 10 min. The low air pressure, short duration of injection, and submersion of the stems in water were to minimize any dehydration of the living cells in

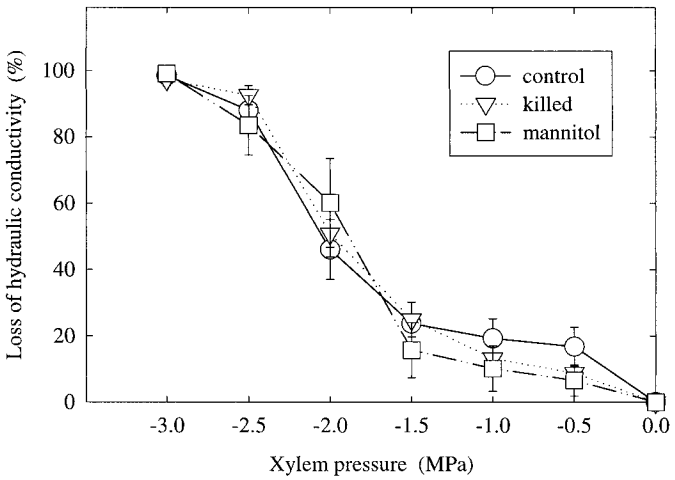


Fig. 3. Vulnerability curves of *Betula nigra* stems for control (circles), killed (triangles), and mannitol (squares) treatments. Symbols indicate mean ± SE, $N = 7$.

control stems that might impair any refilling capability derived from their turgor pressure. The conductivity was measured immediately after the air injection and again after 30 min. Between the conductivity measurements no pressure head was applied, but stems were submerged in water to encourage refilling.

***Statistics***—Data were analyzed with SPSS 8.0 for Windows (SPSS Inc., Chicago, Illinois). We compared vulnerability curves across treatments using a one-way ANOVA (0.05 significance level) for each test pressure. In addition, the mean cavitation pressure was calculated from each vulnerability curve by converting it to a noncumulative distribution that showed the loss of conductivity associated with each pressure decrement. The mean of the noncumulative distribution was calculated using the midpoint of the pressure decrement.

## RESULTS

There was no significant difference between vulnerability curves of control, killed, and mannitol treated stems (Fig. 3). The loss of hydraulic conductivity was only 10–20% for xylem pressures down to −1.5 MPa. Beyond this threshold there was a continual loss of conductivity until −3.0 MPa when stems were completely embolized. The mean cavitation pressure for the pooled data was −1.80 ± 0.29 MPa). This was somewhat more negative than the mean cavitation pressure of −1.65 ± 0.29 MPa reported for juvenile plants of *B. occidentalis* Hook. (Sperry and Saliendra, 1994).

The refilling experiments showed equally slow recovery of conductivity in killed and control stems after a 10-min air injection at 0.1 MPa. Stems showed a 70–75% loss of conductivity immediately after injection, and 30 min later the conductivity was only slightly greater in both treatments.

## DISCUSSION

The results contradict the compensating pressure theory. Vulnerability curves of killed, control, or mannitol-treated stems were identical (Fig. 3) with loss of conductivity occurring between −1.5 and −3.0 MPa for this species. Refilling rates in air-blocked stems were not dif-

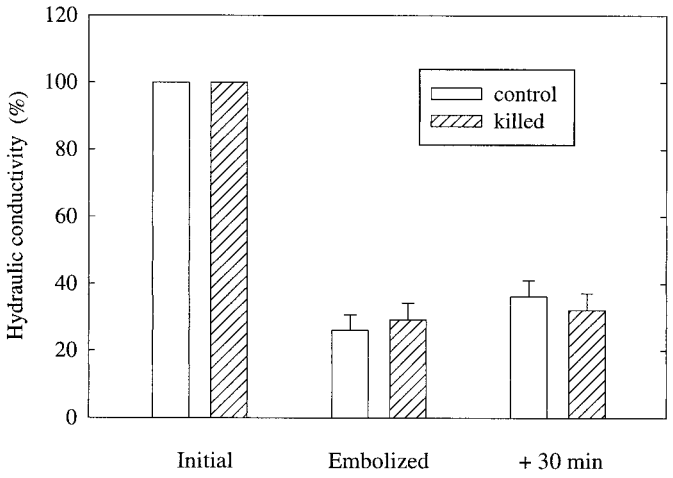


Fig. 4. Hydraulic conductivity of killed vs. control *Betula nigra* stems that were embolized by low-pressure (0.1 MPa for 10 min) air injection. Measurements were before air injection, immediately afterwards, and 30 min afterwards. Conductivity is shown relative to the initial value. Values are mean ± SE, $N = 6$.

ferent in dead or alive stems (Fig. 4). The rates were too slow to influence our ability to detect a loss of conductivity from gas blockage. Refilling by turgid tissue did not occur during the measurement of vulnerability curves. The results add to the already impressive convergence of evidence for the cohesion theory (Tyree, 1997).

The nature of our experimental treatments left little doubt that they would disable any metabolically driven and turgor-dependent refilling mechanism. The killed stems had no respiration whether this was measured immediately after microwaving or 6 h afterwards (Fig. 2A). The cytoplasm of the heated stems was clearly disorganized based on microscopic observation of fresh hand sections. There was no evidence from the conductivity measurements that the xylem became plugged with cytoplasmic debris. The mannitol-treated stems had a water potential of almost 1.5 MPa below controls (Fig. 2B). Although there was no obvious plasmolysis in hand sections of the tissue, it is difficult to conceive how this nonpermeating solute would not have caused a significant reduction in turgor pressure of the stem tissue.

We conclude that vulnerability curves do reflect the true range of cavitation pressures in plants. The cavitation pressure is highly variable depending on habitat, species, and organ. Woody perennial species in deserts are extremely resistant to cavitation, with 100% loss of conductivity in stems occurring as low as −13 MPa (Kolb and Davis, 1994; Sperry, 1995). Plants growing in wetter habitats can be completely cavitated by −1.5 MPa (Tyree et al., 1991). Roots, in particular, appear to be exceptionally vulnerable to cavitation with 50% cavitation at pressures as high as −0.5 MPa (Sperry et al., 1998).

There is no necessary conflict between the available data on cavitation resistance drawn from vulnerability curves and the recent reports of very vulnerable xylem in corn roots and sunflower petioles using a combination of flash-freezing and microscopic observation (Canny, 1997; McCully, Huang, and Ling, 1998). The freezing experiments indicate considerable cavitation at pressures of approximately −0.3 MPa, and they have been used as support for the compensation theory (Canny, 1998a). While it is desirable to make a direct comparison between the two methods, at face value the collective data simply indicate that in some species and organs, some of the xylem can cavitate at relatively high negative pressure. There is no evidence from flash-freezing experiments that all of the xylem is cavitated when it should not be according to the cohesion theory.

Observations of frozen xylem have suggested refilling of the more vulnerable conduits in sunflower and corn within a few hours of their cavitation (Canny, 1997; McCully, Huang, and Ling, 1998). Refilling is not precluded by the cohesion theory and has been documented on several occasions in a wide variety of species (for example, Hacke and Sauter, 1996; Sperry et al., 1994). However, the theory does set lower limits on the xylem pressure allowing the dissolution of gas and bubble collapse, assuming hydraulic contact between the water in the refilling conduit and the surrounding transpiration stream. Under the best of circumstances (a steady stream of gas-free xylem sap running past an air bubble, or a bubble of pure water vapor), refilling could occur for xylem pressures a few kilopascals below the vapor pressure of water (approximately −0.12 MPa relative to atmospheric (Yang and Tyree, 1992).

Refilling under lower pressures has been reported not only for the frozen xylem studies in corn and sunflower (McCully, Huang, and Ling, 1998), but for conifers (Edwards et al., 1994) and dicot trees (Salleo et al., 1996). These interesting findings need more confirmation and study, but do not by themselves require a new theory of water transport. There are a number of possible mechanisms by which refilling could occur in the presence of low negative pressures. These mechanisms could involve the action of living cells, including some of the reverse-osmosis processes mentioned by Canny (1998a) and Milburn (1996). Also required would be a means of isolating the refilling conduit from the water pressure of the surrounding xylem.

To be able to publish in 1998 a paper the purpose of which is to show that plants do generate negative pressures as required by the cohesion theory is an indication of how stubborn the taboo against negative pressure is in some circles. This disbelief persists in spite of over a century of experiment and theory demonstrating the tensile strength of water and the generation of large negative pressures in simple laboratory systems (citations in Pickard, 1981). A branch of physical chemistry is devoted to the study of metastable liquids, including water (Trevena, 1975; Debenedetti, 1996). If Berthelot could generate a negative pressure of −5 MPa in the laboratory glassware of the 1800s (Dixon, 1914), it does not seem unusual that hundreds of millions of years of natural selection could accomplish the same feat in the xylem conduits of plants.

In contrast, the requirements of compensating pressure theory are quite a bit more remarkable and implausible (see Comstock, this issue). According to the theory, once water enters the xylem of the roots, it moves down a gradient in pressure just as in the cohesion theory (Canny, 1998a). The total pressure drop required to overcome gravity and friction in the root-to-leaf xylem path can exceed 1.0 MPa based on transpiration rate and values of

xylem conductivity measured with techniques similar to those in this paper (Tyree et al., 1991, their fig. 7). Although Canny disputed these pressure estimates on the grounds that conductivity measurements are influenced by tissue pressure (Canny, 1998a), our results have shown that conductivity measurements are not influenced by tissue pressure. So, for the compensating pressure mechanism to keep pressures above −0.3 MPa throughout the continuous apoplastic flow path of the xylem (and it typically is continuous; Zimmermann, 1983) while faced with a 1.0 MPa total pressure drop, the xylem pressure at the upstream end would need to be at least +0.7 MPa. Such pressures would cause bleeding from cuts in the xylem, yet this is not seen under transpirational conditions. Furthermore, the squeezing of the xylem conduits required to keep the xylem pressure above −0.3 MPa would only increase the resistance to flow and the pressure drop, leading to a vicious cycle wherein the conduits must be squeezed out of existence. All this assumes that the lignified conduits could be squeezed in the first place by the expansion of turgid parenchyma tissue, when it is known that the bulk of the parenchyma tissue shrinks considerably under dehydrative stress, while the woody lignified tissue tends to maintain its dimensions (e.g., Brough, Jones, and Grace, 1986). In any event, the experiments of Strasburger (1891) showed over a century ago that living tissue was not necessary to sustain the movement of water in the xylem, and our data suggest that nothing has changed since that time.

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