

The Puzzle of Phloem Pressure¹

Robert Turgeon*

Department of Plant Biology, Cornell University, Ithaca, New York 14853

Although transport of organic nutrients and regulatory molecules in the phloem underlies all aspects of growth and development, we still cannot say with confidence that we adequately understand how it is motivated. A major problem is that it is difficult to reconcile the theory of pressure flow, proposed over 80 years ago by Ernst Münch (1927), with transport in large trees. Significantly, phloem pressure does not scale to plant size. Also, the very high turgor in the phloem of herbs suggests that pressure has functions beyond that of sap conduction. A recent resurgence of interest in this field may lead to a fundamental reassessment of the function of phloem pressure in transport physiology.

PHLOEM PRESSURE AND THE MÜNCH HYPOTHESIS: THEORY

According to Münch (1927), long-distance transport is driven by osmotically generated hydrostatic pressure (phloem pressure). Photoassimilates and other solutes enter the source end of the sieve tube and attract water by osmosis. The primary sources are mature leaves. Water and solutes exit in sinks, such as roots and meristematic tissues, resulting in bulk flow of solution.

Theoretical treatments of the Münch hypothesis have long suggested that it adequately explains transport over short distances, but not over the distances encountered in tall trees (see Thompson and Holbrook, 2003a; Jensen et al., 2009b). Recently, Mullendore et al. (2010) readdressed this issue, calculating the expected pressure drop in several species from detailed data on sieve tube anatomy and axial flow velocity. According to their calculations, based on the model of Thompson and Holbrook (2003a), values for specific conductivity (k) in sieve tubes are limited up to 85% by sieve pores and vary by more than 2 orders of magnitude in different plants. Cucurbits, with their large sieve elements and wide sieve pores, have exceptionally high k values ($53 \mu\text{m}^2$; Mullendore et al., 2010), likely as an adaptation to the vine habit. In some species with especially narrow pores, such as *Arabidopsis* (*Arabidopsis thaliana*), k values are as low as $0.22 \mu\text{m}^2$. The fact that conductance is very high in cucur-

bits is important in the sense that it sets an attainable upper limit for comparative purposes with other plants.

The expected pressure drop (Δp) along the sieve tube equals $U\eta k^{-1}$ (Mullendore et al., 2010) where U is axial flow velocity and η is sap viscosity. The expected Δp is 0.008 MPa m^{-1} in *Cucurbita maxima* and 1.0 MPa m^{-1} in *Arabidopsis*. For the purpose of these calculations it is presumed that the sieve pores are open and free of cytoplasm, a reasonable assumption in angiosperms (Knoblauch and Van Bel, 1998), but not in gymnosperms (Schulz, 1992).

With these theoretical calculations in hand, we can now see if there is enough measured pressure in sieve tubes to drive flow. One clear expectation is that, other factors being equal, the sieve tubes of trees should have higher turgor than those of herbaceous plants.

PHLOEM PRESSURE DOES NOT SCALE TO PLANT SIZE

Data do not support the prediction that phloem pressure scales to plant size. Indeed, the opposite appears to be true. It must be kept in mind that these measurements are difficult to make since sieve elements are narrow and secluded in complex tissue. The most reliable method is to take advantage of an aphid's ability to insert its stylet into a sieve element without disrupting flow. Pressure is measured directly by sealing a micropipette over the severed stylet (Wright and Fisher, 1980). Phloem pressure can also be measured with a probe (Hammel, 1968), or calculated from measurements of osmotic and water potentials (Sovonick-Dunford et al., 1981).

Strikingly, the lowest measured values of phloem pressure (0.6–1.4 MPa) are from trees (Hammel, 1968; Wright and Fisher, 1980; Lee, 1981; Sovonick-Dunford et al., 1981). Not all of this pressure is available to drive flow since pressure in sink sieve elements in many organs is at least equal to that of surrounding cells, approximately 0.7 MPa (e.g. Pritchard, 1996). This leaves at most 0.7 MPa to drive transport. Several studies from willow (*Salix* spp.) indicate phloem pressure of approximately 0.7 MPa, which does not allow for any gradient. Lee (1981) measured significant differences in turgor at various elevations in ash (*Fraxinus americana*), but in some cases it was actually higher close to the roots, and Zimmermann's (1957) measurements of sugar gradients in ash can only be reconciled with theory if the pressure in the phloem of the roots is zero.

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* E-mail ert2@cornell.edu.

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The issue of phloem pressure in gymnosperms, some of which transport over exceptionally long distances, is especially acute. In *Pinus strobus*, $k = 4.4 \mu\text{m}^2$ (Thompson and Holbrook, 2003b), which is similar to that of *Phaseolus vulgaris*, assuming that the pores are open. However, there is no way to reconcile the data indicating plugged sieve pores (Schulz, 1992) with Münch pressure flow.

To deepen the mystery, it appears that many tree species do not take advantage of active phloem loading mechanisms to elevate pressure at the source ends of the sieve tubes (Reidel et al., 2009; Rennie and Turgeon, 2009). Two active loading mechanisms have been described: uptake from the apoplast energized by the proton motive force, and polymer trapping (Ślewinski and Braun, 2010; Turgeon, 2010). However, in some species, almost all of which are trees, loading appears to be passive, with no uphill Suc gradient from mesophyll to phloem (Reidel et al., 2009; Rennie and Turgeon, 2009).

It could be argued that turgor measured in stems of trees appears low because it is measured distantly from the leaves in which it is generated. However, osmotic potentials in minor vein sieve elements of poplar (*Populus deltoides*; Russin and Evert, 1985) and willow (Turgeon and Medville, 1998) are considerably lower than those of herbaceous plants.

The analysis above leaves the impression that trees live at the extreme edge of transport capability, with phloem transport motivated by a barely sufficient driving force. However, if this were so, sieve tube conductivity should have evolved to a maximum. It has not. The diameters of sieve pores, the sites of most resistance to flow, are similar in the trees that have been examined to those of most herbs, and well below those of cucurbits (Thompson and Holbrook, 2003b). Photoassimilate travels down the stems to the roots of angiosperm trees at velocities that rival those of herbaceous plants (Plain et al., 2009).

There are two obvious explanations for the discrepancy between theory and data as they pertain to trees. The first is that the discrepancy is more apparent than real. It is possible that technical limitations have led to an underestimation of phloem pressure and conductivity and an overestimation of sap velocity. It is also possible that advances in the theory of flow through tubes with the dimensions and biological attributes of living phloem may lead to a reconciliation between measurements and calculations. In this regard, techniques in microfluidics may better approximate reality than the more macroscopic approaches used to date (Jensen et al., 2009a).

The second possibility is that we are missing something fundamental. For example, it has been suggested that the phloem consists of relays or functional units and that solutes are transported energetically from one unit to the next, providing a boost in pressure at intervals along the transport pathway (Lang, 1979; Aikman, 1980).

The difficulty with the relay hypothesis is that phloem sap is rich in organic molecules and ions

(Turgeon and Wolf, 2009). Transfer across the plasma membrane would require an elaborate set of transporters unless the composition of the sap changes at each step. The long-distance transport of macromolecules (Dinant and Lemoine, 2010) poses a special problem, if they are indeed transported over the entire dimensions of a tree. This issue might not be as pertinent if the relay operates by electroosmosis. As difficult as the relay hypothesis may be to verify, it deserves further attention.

Data are more hospitable to Münch pressure flow in herbs. Phloem turgor is high, even though transport distances are short. For example, pressure readings from aphid stylets indicate turgor of 2.4 MPa in wheat (*Triticum aestivum*; Fisher and Cash-Clark, 2000) and 1.9 MPa in *Sonchus oleraceus* (Gould et al., 2004). For a Δp as high as 0.5 MPa m^{-1} , there is more pressure than necessary to drive translocation. Perhaps the best demonstration of a gradient (0.2 MPa m^{-1} osmotic potential) comes from *Nicotiana glauca* (Hocking, 1980). If one assumes a water potential gradient of 0.1 MPa m^{-1} in the opposite direction, this would indicate a Δp of 0.1 MPa m^{-1} in the direction of flow.

Pressure gradients are difficult or impossible to detect in smaller plants (Fisher and Gifford, 1986; Pritchard, 1996). Indeed, it is striking that available pressure is so much in excess of any detectable Δp between source and sink phloem. In sugar beet (*Beta vulgaris*), the osmotic pressure in importing veins of sink leaves (2.27 MPa) is only 10% less than in source leaf veins (2.52 MPa; Fellows and Geiger, 1974). The excessive turgor in the phloem of small plants suggests that this pressure has additional functions especially suited to the herbaceous growth habit.

WHY IS THE PHLOEM PRESSURIZED?

An obvious advantage to high phloem pressure is that it defends plants. When a sieve tube is wounded, pressure release causes surging and forces cellular debris into the sieve pores, sealing the phloem. Some insects have adapted and can maintain flow with compounds in their saliva (Will et al., 2007), but the majority are confounded by this blunt but effective strategy.

Phloem pressure is also an important factor in regulation. Fisher (2000) describes the phloem as a high-pressure manifold distribution system from which assimilates are bled out of a low-resistance pathway (the sieve tube) by high-resistance leaks (plasmodesmata). This results in uniformity of unloading potential throughout the plant. The principle is apparent in households: Flow from faucets in different parts of a house is similar when pressure in the pipes is high, but differs annoyingly from one faucet to another if pressure drops.

Thompson and Holbrook (2003b) also argue that integrative control over the whole plant is most effective when osmotic strength in sieve tubes is high and Δp along the axis is small. Under these conditions,

localized unloading in a sink automatically reduces turgor everywhere and provides a signal to load more sugar (Patrick, 1994; Thompson, 2006).

Elevated pressure also minimizes the effect of reduced water potential in times of water stress (Smith and Milburn, 1980). The advantages in maintaining an uninterrupted supply of nutrients and phloem water to meristematic zones, and the pressure needed for effective regulation, are obvious.

Another way to view excessively high phloem pressure is that it is a secondary consequence of active loading, not its primary purpose. Active loading increases the concentration of transport solute in the sieve tubes, discouraging phloem feeders by creating osmotic potential high enough to desiccate animal tissues. Aphids have strategies to reduce the osmotic potential of the sap in their gut (Ashford et al., 2000), but not all insects have this capability. Also, by increasing the soluble carbohydrate content in sieve tubes, the amount of carbon and energy delivered per unit volume rises and the amount of excess water that has to be dealt with by sinks, especially dry seeds and fruits, is minimized. The trade-off is that viscosity increases with concentration, reducing flux. Lang (1978) calculated that the optimum Suc concentration is 0.75 M, a level that can only be achieved by active loading.

Another advantage to active phloem loading is that it allows plants to reduce inventory of nonstructural carbohydrates in leaves without compromising export (Turgeon, 2010). This strategy frees up reduced carbon compounds to make new leaves. Decreasing unnecessary inventory increases relative growth rate by accelerating formation of new leaves. It is possible that active loading evolved along with the herbaceous growth habit to reduce foliar inventory, resulting in more rapid growth and, incidentally, the additional benefits described above.

CONCLUSION

The fact that we are still puzzled by fundamental aspects of phloem transport physiology testifies to the subtleties of the mechanisms involved and the technical difficulties associated with conducting experiments on such a reclusive and unaccommodating tissue. A continuing problem in this field is that only fragmentary information is available for individual species and we are therefore forced into making generalities about an ideal plant when it is clear that each parameter, such as sieve pore width, is part of a species-specific adaptive strategy. More comprehensive studies on the physiology and quantitative anatomy of selected species are called for (Thompson and Wolniak, 2008; Mullendore et al., 2010), recognizing that there may be fundamental differences in underlying processes in different plant types, especially trees and herbs. Gymnosperms are particularly puzzling in many respects and deserve more attention.

Available data suggest that the amount of phloem pressure, and the anatomical parameters that define conductivity, have been evolutionarily optimized in both woody and herbaceous plants for several purposes, only one of which is to motivate long-distance transport.

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