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Commentary

Phloem transport in trees

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Phloem is like an enigmatic central banker: we know how important phloem is to plant function, but very little about how phloem functions as part of a whole-plant economy. Phloem transports carbohydrates, produced by photosynthesis and hydrolysis of reserve compounds, to sink tissues for growth, respiration and storage. At photosynthetic tissues, carbohydrates are loaded into phloem (Rennie and Turgeon 2009), a process that raises the solute concentration. This increased solute concentration then raises turgor pressure in the transport stream by drawing water from the xylem through osmosis. At growth and storage sinks, carbohydrates are actively unloaded or passively leak out of phloem, lowering the solute concentration. Water then moves back into the xylem from the phloem, lowering turgor, and the turgor pressure difference between the loading and unloading sites drives the mass flow of carbohydrates to the sink tissues. This simple mechanism of turgor-driven transport, first hypothesized by Münch in 1927 (Münch 1930), connects source and sink tissues, automatically delivering photosynthate to sink tissues with the lowest concentrations and thus the highest consumption rates and need.

Turgor-driven phloem transport as simplified into a mathematical model can explain phloem transport for short distances (Christy and Ferrier 1973) and distances of up to 5–10 m (Thompson and Holbrook 2003). For a tree, these models would predict that phloem turgor pressure at the source would need to increase with canopy height to overcome resistances caused by transport distance (Thompson and Holbrook 2003). Consequently, the phloem of tall trees in the upper canopy would need higher turgor than herbaceous plants and a greater difference in turgor between the upper canopy and roots for effective carbohydrate transport.

Though very few data exist to test them, these predictions are unsupported. Phloem turgor pressure is low in some trees (Sovonick-Dunford et al. 1981), too low to drive photosynthate out of the phloem (Turgeon 2010), and phloem turgor changes little to none with height in other trees (Hammel 1968, Lee 1981). More measurements are needed, but the turgor pressure itself complicates these measurements. Because phloem is pressurized, puncturing or damaging the phloem in an attempt to measure it causes a sudden release of pressure and alters phloem anatomy and thus the phloem pressure itself (Turgeon and Wolf 2013). Also, because phloem consists of live tissues, an attempt to measure it often induces wound reactions (Ehlers et al. 2000, van Bel 2003), contributing to the lack of data. However, tall trees exist and their roots are supplied with carbohydrates despite the fact that our understanding, models and measurements suggest that they should not. This disconnect between theory, data and tree behavior suggests that phloem transport in trees is a fertile area for research.

Woodruff (2014) examined a problem in tree phloem physiology that is important for understanding transport in tall trees and also for understanding how drought might impact phloem anatomy, phloem sap viscosity and carbohydrate transport. The study examined how sieve cell radius, sap sugar concentration, phloem relative water content and sap viscosity might vary with mid day leaf water potential under well-watered soil water conditions in tree tops, with tree height varying from 2 to 57 m. Tree height generated a strong gradient in mid day leaf water potential from -1.2 MPa in 2-m-tall trees to -1.8 MPa in 57-m-tall trees. Because this gradient was assessed under well-watered conditions with low evaporative demand, we can assume that these water potentials are near the minimum that will be attained during a diurnal cycle under

well-watered conditions, and near the maximum for a seasonal cycle that includes a long summer drought. Sieve cell lumen radius declined by 20% with increasing height, from 9.5 μm in 2-m-tall trees to $\sim 7.5 \mu\text{m}$ in 57-m-tall trees, and the decline was linear with the well-watered spring pre-dawn leaf water potentials. The relative water content of the phloem also decreased by $\sim 20\%$ under similar conditions. Sieve cell sucrose and total sugar concentration did not vary with sample height, but glucose + fructose concentration increased with sample height. Accounting for sugar concentration and water content, the sap viscosity and molar concentration of sucrose did not vary with tree height, but the viscosity and molar concentration of total sugars increased with sample height. Combining the decreased sieve lumen diameter and increased viscosity resulted in a 60% reduction in conductivity (modeled with the Hagen–Poiseuille equation) with increased tree height.

The Woodruff (2014) study strongly indicates that phloem transport has to overcome increasingly more difficult conditions as trees grow taller. Combining the results from this study with the difficulties of an increasingly long path length (Thompson and Holbrook 2003) suggests large and increasing limitations to phloem conductivity as trees grow taller under our current paradigm. Could increases in phloem conducting area with height compensate or partially compensate for a decreased phloem conductance per unit of phloem area? For example, lower leaf area to sapwood area ratios and lower mid day leaf water potentials with tree height can sometimes partially compensate for the increased path length and gravitational potential as trees increase in height (McDowell et al. 2002, Ryan et al. 2006). This would be an interesting hypothesis to test, and the few existing measurements show that phloem area increases with age/size and is related to an increase in xylem sapwood area, and thus the ratios of leaf area to phloem and xylem both decrease but less so for the phloem (Ewers and Fisher 1991, Mencuccini et al. 2011). More studies will help to clarify the question of compensation in phloem area with tree height. Fluxes of carbohydrates to all components of a tree decline with increasing tree height (Ryan et al. 2004, Drake et al. 2011), and this phenomenon has been related to reduced photosynthesis (Ryan and Waring 1992, Ryan et al. 2004, Drake et al. 2011), but the role of sink limitation (Woodruff et al. 2004) and feedbacks to photosynthesis (Paul and Foyer 2001) or phloem transport limitations (Woodruff 2014) remain to be explored. Separating cause from effect would require concurrent measurements of canopy photosynthesis and fluxes to respiration, growth and storage—a daunting task for large trees (Ryan 2011).

Because of the difference in water potential from gravity, tree height may also be a surrogate for the response of shorter trees to lower soil water potentials. A more negative water potential generated by drought would likely generate lower tur-

gor pressure in phloem, as has been found with the lower water potential as tree height increases (Woodruff 2014). Because cell division and expansion are sensitive to turgor pressure (Hsiao 1973), fewer and narrower phloem cells might be produced under a lower leaf water potential regardless of the cause. Phloem relative water content, viscosity and sugar concentration might also reasonably be expected to change with drought in a similar manner as with tree height, leading to lower phloem conductivity. What we do not know is whether phloem cell division and expansion in tall trees has somehow adapted to the chronically low water potential, nor do we know whether phloem in tall trees would be less able to osmotically adjust to a lower water potential than phloem in shorter trees. Such adjustments may even be unnecessary—gravity is an obstacle in xylem transport, but it may aid phloem transport in tall trees by reducing the viscosity and osmotic pressure required to push phloem fluid down to the roots (Hölttä et al. 2009). We also currently have only poor means of assessing whether conductivity modeled from phloem radius and viscosity matches actual conductivity.

Because of the difficulties in measuring phloem function, particularly in trees, we lack a basic natural history and phenomenology of tree phloem. What little research exists has focused primarily on cellular structure and mechanisms and an exploration of theory (e.g., van Bel 2003, Thompson 2006, Turgeon and Wolf 2013). However, some advances in measurement techniques, theory and a whole-tree approach may help address this important component of tree structure and function.

New techniques for assessing phloem turgor and flow have been developed, and these show promise. Phloem turgor may be measured without damage by tracking changes in tree diameter with and without phloem tissue complexes (Sevanto et al. 2011). Phloem transport rates may be measured by pulse labeling of CO_2 and tracking the respiration stream (Högberg et al. 2008, Plain et al. 2009, Dannoura et al. 2011, Epron et al. 2012), or by tracking the changes in bulk soil CO_2 flux (Stoy et al. 2007). Data from these studies indicate that photosynthate may travel from leaves to roots in a matter of days (Mencuccini and Hölttä 2010). A new non-destructive laser-heat-pulse technique for measuring phloem flow has also been developed (Helfter et al. 2007).

Data from these measurement techniques, however, highlight the need to consider phloem transport theory at the whole-tree level. Mencuccini and Hölttä (2010) found that a coupled phloem–xylem transport model predicts that phloem transport rate will vary with path length. Therefore, tall trees must have much higher phloem-specific conductivity and generate greater turgor pressure differences than short trees to explain the observed transport rates. But neither of the phloem studies in tall trees support these requirements (Woodruff et al. 2004, Woodruff 2014), suggesting that our current

understanding of long-distance phloem transport in tall trees is incorrect. Additional studies suggest that the Münch pressure-flow model of phloem transport may not apply at the whole-tree level (Young et al. 1973, Thompson 2006, Turgeon 2010), raising the question of how trees sense turgor pressure differences between phloem loading and unloading sites over many meters, if at all (Thompson 2006).

These questions have led to theoretical approaches that scale phloem function to the whole-tree level (Hölttä et al. 2009, Jensen et al. 2012), couple xylem and phloem functions (Hölttä et al. 2009), and link gas exchange, fluid transport and soil diffusion (Mencuccini and Hölttä 2010). These approaches find that large turgor pressure differences are not necessary to drive flow in tall trees if phloem is tapered enough to minimize resistance with increased path length (Jensen et al. 2011, 2012, Mencuccini et al. 2011). Other studies argue that faster phloem transport can be achieved if phloem in trees is considered as relays of segmented tubes and not as continuous from leaves to roots (Lang 1979, Hölttä et al. 2009, De Schepper et al. 2013). These studies together indicate that basic questions of the mechanism and control of phloem transport rate in trees remain to be answered.

Our knowledge of the coordination of phloem with whole-tree function remains primitive. Perhaps simple metrics of phloem, such as that accomplished in the Woodruff (2014) study, might rapidly expand our knowledge to answer such simple questions as: What is the phloem area for a tree and stand? What is phloem conductivity relative to demand? Is there a link between phloem area or phloem conductivity of a forest, and partitioning or flux to stem and root sinks? Is there a link between phloem area or phloem conductivity and canopy photosynthesis and/or light-use efficiency? Do phloem area or phloem conductivity differ among species or with stand age? Such studies would help make our 'central banker' less enigmatic.

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