PHLOEM TRANSPORT IN TREES

# Zero-calorie sugar delivery to roots

Resistance to moving sugars from foliage to roots is high in trees, suggesting that the transport mechanism found in herbs might not work in trees. Now with new measurements of phloem structure and leaf turgor pressure, it has been shown that the Münch pressure-flow hypothesis can also explain sugar transport in tall trees.

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Sugars move through phloem conduits from the leaves to the stem, branches and roots to supply energy and material for tissue construction, maintenance and ion transport. The motive power for phloem flow arises from the greater turgor pressure in leaf phloem than in the destination, as a result of the greater sugar concentration in the leaves. This simple mechanism of turgor-driven transport was first hypothesized by Münch in 1927[1] and automatically delivers sugars to tissues with the lowest sugar concentration and highest need. For tall trees, there was a fundamental question about the viability of Münch flow: how can transport overcome the large frictional resistance in the small phloem conduits and in the sieve plates that separate the conduit elements[2]? Resistance to flow will increase with path length, and trees tend to load phloem passively (unlike herbs, which actively load sugars against a concentration gradient), so they are unlikely to generate high turgor pressure. Phloem cell size could be limited to remain connected to companion cells, constraining reductions in resistance[3]. The necessity to seal punctures and reduce leaks also argues for lower turgor pressure[4]. Because of these issues, other mechanisms for movement in phloem that require energy — active transport and cascading loading and unloading — have been proposed as alternative mechanisms

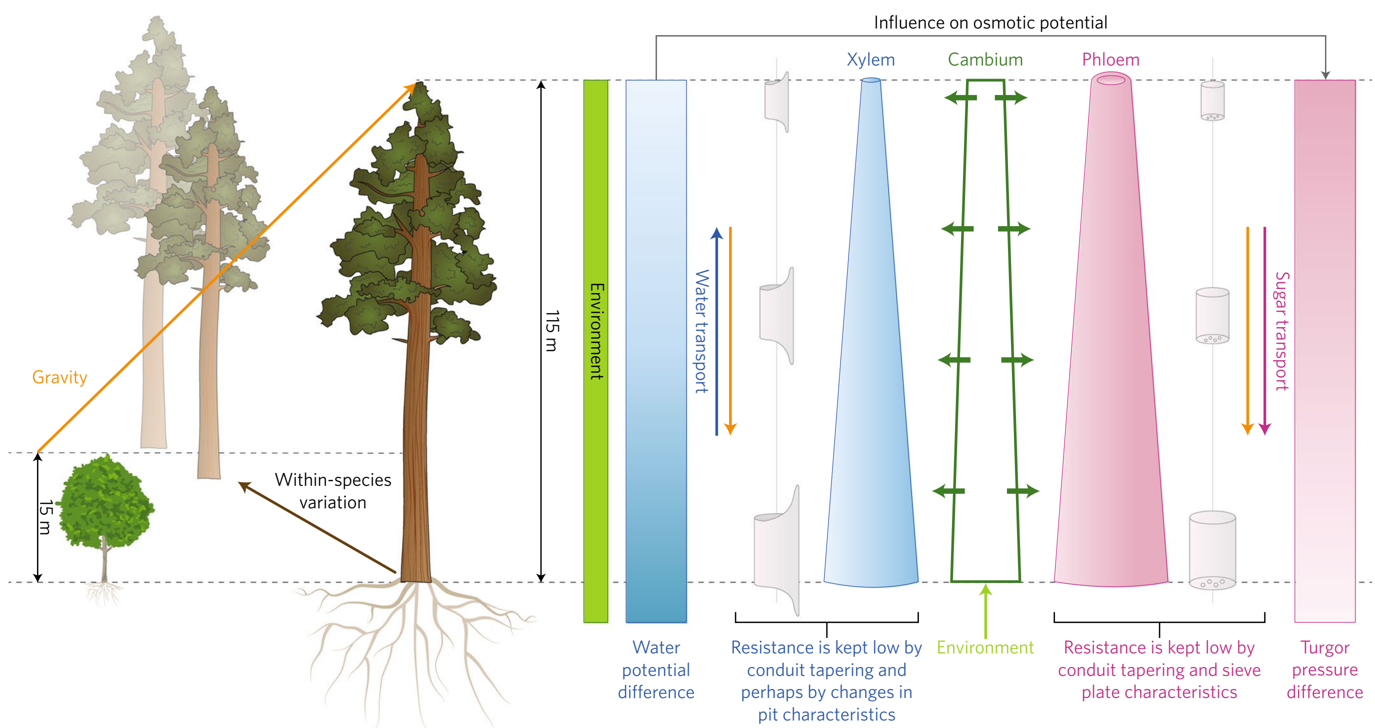


**Fig. 1 | Vascular transport in tall trees.** Phloem sugar transport in tall trees by Münch turgor pressure flow relies on larger conduits and wider pores in the sieve plates. Water is transported inside the plant xylem (blue cone) and sugars are transported in the phloem (pink cone). These two tissues are separated by the cambium (dark green), which produces both xylem and phloem cells. Xylem water moves upwards along a water potential gradient, while phloem sugars move downwards along a turgor pressure gradient (indicated by the coloured shading for each mechanism bar). Tall trees are subject to gravity forces (orange arrows), in proportion to their height, that aid sugar transport but impede water transport. Gravity may be important for the tallest trees shown in this figure. The long-distance transport of water and sugars is facilitated by basipetal widening of xylem and phloem conduits, as well as widening of the sieve plate pores inside phloem conduits (small conduit elements on both sides). As individual xylem and phloem tubes widen from the top to the base, their total area also widens, provided that the number of tubes does not change. Decreased resistance and increased area from top to bottom lead to the overall cone shape of the resistance. The environment and species can affect the behaviour of all three systems — xylem, cambium and phloem — leading to variability seen in the field (brown arrow).

in trees. Using new techniques[5,6] to image and measure pores in sieve plates and turgor pressure in situ, Savage et al.[7] show in this issue of *Nature Plants* that phloem resistance declines along the flow path from leaf to root in several species of temperate broadleaf trees (Fig. 1). Coupling the measurements of phloem pressure in leaves with estimates of phloem flow speed that incorporate the measured decreased resistance shows that this decreased resistance is necessary and sufficient for moving sugars from the tops of tall trees (> 20 m) to the roots, as proposed in earlier theoretical models[8].

The lack of measurements of phloem anatomy and pressure has long hampered progress on the issue of whether passive loading and transport through the long phloem tubes of tall trees is possible. The phloem radius at the tree base can increase with tree height, as is shown in xylem[9,10]. But the opening size and number of sieve plate pores are also an important component of resistance, and this resistance has been mostly unknown because of the difficulty in imaging them. Measurements from scanning electron microscopy of imaged sieve plate pores showed that phloem conduits get wider and longer and sieve plates have wider pores when moving from the top to the bottom of trees. Therefore, resistance in the phloem conduits per unit length decreases with height of the tree. Modelled conductance for a single tube from the top to tree bottom using this phloem anatomy reduces the pressure required for sugar transport to below the turgor pressure measured at the leaf in situ with pico gauges. If phloem had the smaller size and pore openings measured at the top of the trees for its entire length, the pressure required to produce flow would be substantially more than could be generated by passive loading of sugars.

The sieve plates matter: the resistance of the sieve plates was more than half of the total resistance, and scaled proportionally with the resistance generated from the radius and length of the conducting elements. Both xylem and phloem conduits varied similarly with height, with wider, longer cells near the tree base. Phloem resistance per conduit is approximately ten times greater than xylem vessels because the conduits are much narrower than the xylem cells.

Phloem anatomy changes for all the species measured, suggesting that decreasing resistance from leaves to roots is a common, perhaps even universal, solution for moving sugars in tall trees via turgor-driven mass flow. The Münch pressure flow model is such a simple, elegant mechanism for sugar transport; that it can work in tall trees solves a mystery that has endured for many years.

Future work should examine conifers, as well as the tallest of trees, which can be up to 115 m tall. Phloem conduits also widen towards the base of conifers[10], but examining sieve pore changes in conifers would assess if the relationship between sieve plate and conduit lumen resistance is general. An increase in phloem area down the stem could also reduce whole-tree phloem resistance. Xylem area increases from tree top to bottom, and so might phloem area. Relating phloem area to leaf area (as in water flux studies) might also be helpful in estimating whole tree fluxes. Gravity is important in tall trees, as it should aid phloem sugar flow and hinder xylem water flow. Linking phloem and xylem flow is probably also important, as the water potential of the xylem affects the osmotic potential of the phloem[11]. Such linkage may provide another challenge for taller trees compared with the simple phloem tube top-to-bottom model used in this study. Finally, annual water availability and temperature strongly change annual xylem production. Do the same signals affect phloem growth and anatomy? ❐

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Competing interests

The authors declare no competing financial interests.