

Chapter 2

Ecophysiological Aspects of Phloem Transport in Trees

Teemu Hölttä, Maurizio Mencuccini, and Eero Nikinmaa

Abstract The primary function of the phloem is the transport of assimilate products from mature leaves to other tissues. Here we examine this function from a whole tree perspective and relate it to assimilate production, tree water relations, and tree structure. We argue that the turgor and osmotic pressures driving flow in the phloem are determined by these factors. An example calculation of these interactions is presented. The generalizations and possible shortcomings of the Münch flow hypothesis, the simplest theoretical framework used in describing phloem transport, are also discussed.

2.1 The Münch Flow Hypothesis

Long distance transport of water from soil through the xylem to the leaves is a fairly well understood process (see [Chap. 6](#)), but the long distance transport of assimilate products in the adjacent phloem tissue is a much less understood, and a more complicated process. The formulation of the theory of phloem transport is acknowledged to date to the work by Edward Münch in the 1930s, although very similar ideas were already developed in the nineteenth century (reviewed in Knoblauch and Peters [2010](#)). According to the Münch flow hypothesis, sugars produced in leaf mesophyll cells are loaded into the sieve tubes in the phloem. Sugar loading can be an active process, or it can happen passively along a concentration gradient, depending on the species (Turgeon [2010](#)). This loading decreases the osmotic

T. Hölttä (✉) • E. Nikinmaa

Department of Forest Sciences, University of Helsinki, PO Box 24, 00014 Helsinki, Finland
e-mail: teemu.holtta@helsinki.fi

M. Mencuccini

School of GeoSciences, University of Edinburgh, Crew Building, West Mains Road,
Edinburgh EH9 3JN, UK

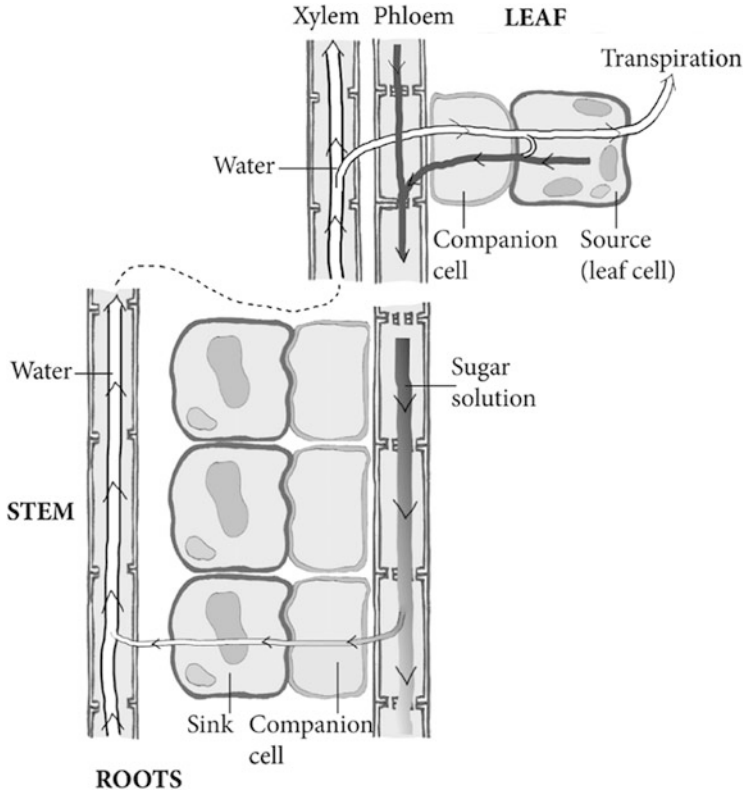


Fig. 2.1 A schematic presentation of the Münch flow hypothesis. Sugars are loaded into the sieve tubes of the phloem at the sugar source (leaf). The osmotic pressure of the sieve tubes is decreased; water is taken up from the surrounding tissue, which results in an increase in turgor pressure at the source. Unloading of sugars from the sieve tubes at the sinks (stem and roots) increases the sieve tube osmotic pressure, water escapes to surrounding tissue, and turgor pressure is reduced. The turgor pressure gradient between the source and the sink is the driving force for phloem transport. Phloem function is linked to xylem transport as water circulates between the two tissues. Phloem takes up water from the xylem along the whole transport pathway unless sugar unloading is locally very large. The transpiration stream in the leaves can also pass apoplastically along the cell walls without crossing the membrane of cells (Figure drawn by Kari Heliövaara, University of Helsinki)

potential of the sieve tubes, which results in water flow from the surrounding tissue, and a subsequent increase in turgor pressure. The active unloading of sugars from the sieve tubes at the sinks decreases the sieve tube osmotic concentration, resulting in water efflux and a reduction in turgor pressure. This turgor pressure gradient between the source and the sink is the driving force for phloem transport. According to the Münch flow hypothesis, sieve tubes are thought to be symplastically continuous along the whole plant axis, and the phloem sap flow totally passive outside the source and sink areas. The Münch flow hypothesis is depicted schematically in Fig. 2.1.

2.1.1 Possible Shortcomings of the Münch Flow Hypothesis

There are doubts over whether the Münch flow hypothesis alone is sufficient to explain phloem transport. According to the hypothesis, active processes are only required at the sources and sinks, and the transport pathway is assumed to be passive (non-energy consuming). Many experiments have demonstrated that this is not fully the case, as for example metabolic impairment of the transport phloem by cold blocking or metabolic poisons has been shown to affect phloem transport dramatically (e.g., Peuke et al. 2006). Continuous leakage and reloading of solutes has been observed along the phloem translocation pathway (Minchin and Thorpe 1987; McQueen et al. 2005).

Doubts over the role and significance of passive phloem transport have been expressed, especially for trees due to long transport distances. In the case of tall trees, the turgor pressure difference required to drive phloem flow between the sources and sinks, and the speed of information transmission between the sources and sinks, could become quite large based on standard theory (Thompson 2006). Experimental tests of the basic tenet that the turgor pressure gradient will drive solution flow in a compartment bounded by semipermeable membranes are difficult to conduct at realistic micrometer scales. Jensen et al. (2010, 2011) used lab-on-a-chip technology to develop a system with dimensions approximating those of real sieve elements (50–200 μm) and experimentally verified that osmotic gradients can generate large enough pressure gradients to move the solution at speeds predicted by the theory.

2.2 Relationships Between Whole-Tree Transport of Assimilated Sugars, Phloem Turgor Pressure, and Osmotic Concentration

A turgor pressure gradient in the phloem sieve tubes is required to overcome the frictional resistance between the phloem sap and sieve tubes walls and the sieve plate pores between adjoining sieve tube elements. An important issue in reconciling phloem transport with the Münch flow hypothesis is the magnitude of these turgor gradients and the flow rates maintained in the sieve tubes (e.g., Thompson 2006). The pressure difference required for the transport of photosynthates from the leaves can be approximated from simple equations, provided that the structural characteristics of the phloem are known. The transport rate of sugars in the phloem sap is proportional to the turgor pressure gradient times the concentration of the phloem sap. The relation can be expressed mathematically as follows:

$$J_s = \frac{\Delta P}{l} c \frac{kA}{\mu} \quad (2.1)$$

ΔP is the turgor pressure difference between the sugar source and sink, l is the distance between the sugar source and sink, c is sugar concentration, k is phloem specific conductivity, A is phloem cross-sectional area, and μ is phloem sap viscosity.

Unfortunately there are no direct measurements of phloem specific conductivity k , but from anatomical measurements of sieve tube diameter and the size and number of the sieve pore plates adjoining the tubes, it has been estimated to vary in the range of 0.22–56 μm^2 among different species (Thompson and Holbrook 2003; Mullendore et al. 2010). The specific conductivity ranged between 4 and 12 μm^2 among the tree species studied. Confirmations of these theoretical calculations are missing since there are very few simultaneous measurements of flow rates and turgor pressure gradients (but see Gould et al. 2005). For example, it is uncertain how open the sieve plate pores are in their natural state.

There is another restriction to phloem transport, which relates to the water exchange with the adjacent tissues. Sieve tube water potential has to be nearly in equilibrium with the water potential of the surrounding tissue, which is determined mainly by xylem water transport, at least in the case of trees. Neglecting radial water potential losses (Thompson and Holbrook 2003), a relationship between phloem turgor pressure, osmotic concentration, and xylem water potential is established:

$$\Psi = P - \sigma cRT \quad (2.2)$$

Ψ is the water potential of surrounding tissue (xylem), P is phloem turgor pressure, c is the osmotic concentration in the sieve tube, R is the gas constant, T is temperature and σ is the reflection coefficient of the membrane separating the sieve tube from its surroundings. Often σ is assumed to have a value of 1, i.e. that of a semipermeable membrane. All of the variables in these equations can be dependent on the axial position along the phloem transport system, so that solving for the pressure and concentration as a function of height is a complex problem, especially as viscosity is highly concentration dependent. To demonstrate the calculation of the phloem turgor pressure gradient, a simplified approach can be taken in which the equations are solved only at one position, i.e. the axial variability in the variables is ignored. Adopting this approach, and assuming that all sugars produced by photosynthesis are transported from the leaves to the soil, a unique solution for the turgor pressure and sugar concentration can be obtained from Eqs. 2.1 and 2.2. This is done here numerically, based on values at the source, as the concentration dependency of viscosity makes the equations impossible to solve analytically.

The turgor pressure at the top of our model tree is approximately 1.0 MPa (Fig. 2.2a), leading to a turgor pressure difference of 0.5 MPa between the source and sink. The osmotic concentration at the source is approximately 800 mol m^{-3} (Fig. 2.2b). Both of these values increase with decreasing phloem permeability and

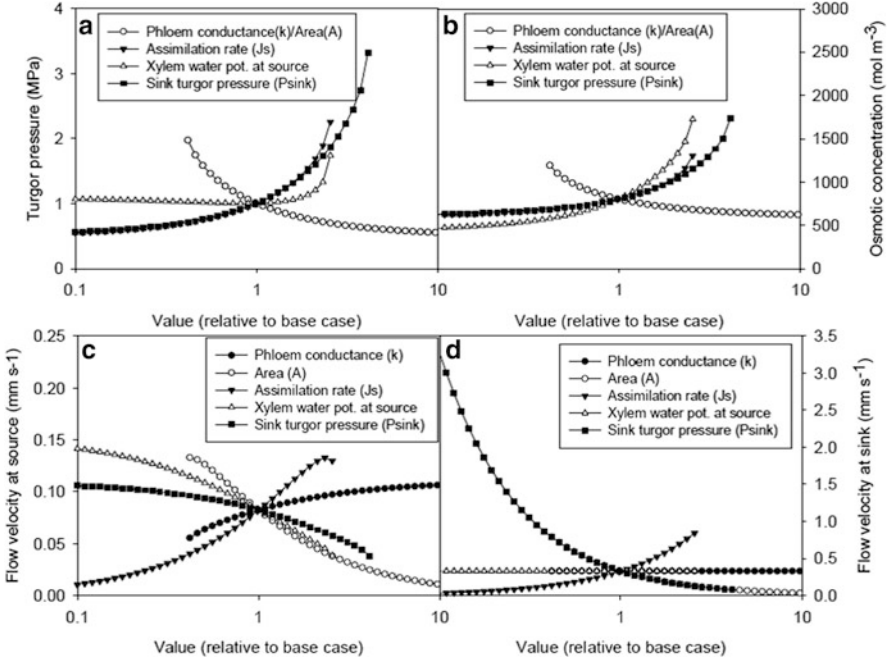


Fig. 2.2 The turgor pressure (a) and osmotic concentration (b) at the source phloem, and the phloem sap flow velocity at the source (c) and sink (d), and their changes when phloem parameterization (in Eqs. 2.1 and 2.2) is altered. The parameter values used in the base case calculation are as follows: tree height (h) 10 m, phloem cross-sectional area (A) $0.25 \times 10^{-3} \text{ m}^2$ (which equates to 1 mm thick phloem on a 0.16 m diameter stem), phloem permeability (k) $4 \mu\text{m}^2$, whole tree assimilation rate (J_s) $17 \mu\text{mol s}^{-1}$ of sucrose, xylem water potential (ψ) at source and sink -1 and 0 MPa , respectively, and a sink turgor pressure (P) 0.5 MPa . Phloem sap viscosity μ was made a function of sugar concentration. The parameter values for which no values can be found in the graph (e.g. low conductance/phloem cross-sectional area) represent cases where the phloem cannot transport all assimilated sugars. Tree height was not varied because a change in tree height is likely to lead to simultaneous changes in almost all of the parameters. In (a) and (b), changes in phloem conductance and phloem cross-sectional area both produce exactly the same changes, and are therefore not drawn separately

phloem cross-sectional area, and with increasing whole tree photosynthesis rate and sink turgor pressure. The turgor pressure and osmotic concentration at the source increase with decreasing xylem water potentials. The turgor pressure also slightly increases at very high xylem water potentials as the phloem sap gets diluted with regard to sugar concentration. The values for the turgor pressure gradient and osmotic concentration are in agreement with measured values (Turgeon 2010). The resulting phloem sap flow velocity is approximately 0.1 mm s^{-1} at the source (Fig. 2.2c), but it increases considerably towards the sink (Fig. 2.2d) to compensate for the decreasing sugar concentration towards the sugar sink, as the sugar flux rate is the same everywhere. In our example base case calculation, the osmotic concentration at the sink is only one fourth of the osmotic concentration at the source, and

the flow velocity therefore is five times higher, i.e. 0.3 mm s^{-1} , which is very similar to values found in experimental NMR studies (e.g., Windt et al. 2006). The sap flow velocity is also sensitive to the parameter choices: it increases with increasing phloem conductance and assimilation rate, and with decreasing phloem cross-sectional area, xylem water potential and sink turgor pressure (Fig. 2.2c, d).

Note that the solution presented is the only possible (stable) solution to Eqs. 2.1 and 2.2. Therefore, no other combination of values of turgor pressure (or its gradient) and osmotic concentration is possible in steady state. For example, a change in turgor pressure at any point along the pathway would lead to a perturbation from steady state, and the turgor pressure gradient would eventually (although not necessarily very quickly), have to return back to the steady state solution. This could also indicate that it is not the pressure difference that controls the flow rate, but rather the flow rate is determined by the transport needs of the plant, which determines the whole tree pressure gradient, as hypothesized by Knoblauch and Peters (2010). This could be compared to the situation in the xylem. It can be argued that the xylem water potential gradient does not control the xylem sap flux rate. Instead, the xylem water potential gradient is determined by xylem conductance and the evaporative demand of water, which is tightly controlled by the stomata in the leaves.

However, it seems possible that plants could exert control over phloem conductivity, and therefore be able to “tune” the values of plant turgor pressure and its gradient. Phloem conductivity is likely to be very dependent on the effective radii of the sieve pores and other obstructions to flow, which could be modified very quickly (Thorpe et al. 2010). It also seems possible that the phloem conducting area varies over time (Windt et al. 2006). Theoretically, a modification in phloem conductivity and flow conducting cross-sectional area would change the turgor and osmotic pressures and could therefore act as a mechanism to control the turgor pressure and osmotic concentrations in the phloem. In addition, there could be many other ways for a plant to regulate turgor pressure in the short term, such as changes in the reflection coefficient of the sieve tubes (see Eq. 2.2) or the active loading and unloading of sugars along the phloem transport pathway.

2.2.1 Speed of Link Between Phloem Sources and Sinks

One peculiar feature of phloem transport is that the propagation of changes in sugar concentration is predicted to occur faster than the movement of the individual sugar molecules themselves. The situation arises since the driving force for the advection-driven phloem transport is created by the substance itself, i.e. sugar. This can be predicted from the mathematical formulation of the Münch flow hypothesis (e.g., Ferrier et al. 1975; Thompson 2006), but its demonstration is beyond the scope of this chapter. Increase in sink sugar concentration due to source action can occur before the actual sugar molecules have traveled from the source to the sink. The experimental evidence for sugar concentrations propagating faster than individual

sugar molecules is scarce, probably since the measurement of phloem sugar concentration dynamics is very difficult. However, a meta-analysis by Mencuccini and Hölttä (2010) revealed that the time lag between a change in photosynthesis rate and a change in soil or ecosystem respiration rate was on average shorter, and much less dependent on transport distance, than the transit time of individual, isotopically marked molecules. Faster propagation of changes in sugar concentration could be important as it allows sinks and sources at different parts of the plant to sense changes in other parts. A reader interested in the time scales associated with the speed of link should turn to Thompson (2006), for example.

2.2.2 Tree Size and Phloem Transport

Since large transport distances are hypothesized to lead to large pressure differences between the sources and sinks and to a slow propagation of molecules and information between the sources and sinks, how can tall trees cope with the challenges of transporting photoassimilates? An increasing turgor pressure difference with increasing transport distance could be inferred simply from Eq. 2.1: the turgor pressure difference necessary to transport a given amount of solution is linearly proportional to transport distance, provided that the cross-sectional area and permeability remain constant. Experimental evidence of turgor pressure gradients in trees and especially its scaling with tree size is very limited. Turgeon (2010) claimed that some indications exist that the turgor pressure differences between the sources and sinks do not scale with tree size. On the contrary, calculations by Mencuccini and Hölttä (2010) from a meta-analysis of time lags between photosynthesis and soil respiration pointed towards phloem pressure gradients (calculated from the observed time-lags) increasing with plant size, although in the final statistical analysis the calculated rate of change in pressure gradients with tree size was highly correlated with the corresponding rate of change in specific conductivity, making their separation difficult.

Very little is known about the variation in phloem conduit properties and flow conducting area with changing tree size and axial position. In the neighboring xylem tissue, the water potential difference between the leaves and roots (which is equivalent to the turgor pressure difference in the phloem as the driving force for transport) normally does not differ much between small and tall trees. It is therefore evident that conduit properties must change with tree size so that sufficient water supply to the leaves is maintained with increasing transport distance. This is achieved by an increase in xylem conduit size according to a power law to prevent the loss of water transport capacity due to increased transport length (West et al. 1999). This general scaling theory also suggests that a similar principle must apply to phloem conduits to compensate for the increasing transport distance with increasing tree height, but very few studies have been made to address this topic directly. Perhaps the only systematic study was the one conducted by Mencuccini et al. (2010), who found that phloem conduits did increase in size

with increasing tree size, therefore alleviating the problems of phloem transport over long distances.

Changes in the phloem cross-sectional area may also influence phloem transport. However, quantitative measurements of conducting area along the stem axis are rare. Along the stem height, the actual thickness of conducting phloem cells seems to be fairly constant (Quilho et al. 2000), while the cross-sectional area of water conducting wood increases clearly from the stem top towards the base. This means that along the conducting axis, the ratio of phloem to xylem tissue increases towards the leaves, being close to one in leaf veins. Hölttä et al. (2006) showed that such a structure can maintain higher phloem loading rates than if the proportions were equal along the entire axis.

An alternative mechanism that would allow trees to overcome the problems of long transport distances is the use of the so-called solute relays. If solute relays were present, the sieve tubes would not be symplastically connected over the whole transport distance, but there would be loading and unloading of sugars at specific points along the transport pathway (Lang 1979). The pressure difference and the speed of information transmission within a tree would then decrease in approximately linear proportion to the number of relays (Hölttä et al. 2009). Lang (1979) estimated that approximately 2 % of the transported sugars would be used up in each relay because of the metabolic cost of unloading and reloading. Hypothetically, this metabolic cost could be compared with the cost of building larger or more phloem sieve tubes without relays to achieve identical sugar translocation rates. However, there is no substantial experimental evidence either in favour or against the existence of solute relays.

2.3 Connections Between Phloem and Xylem Transport

While xylem transport must occur against gravity, phloem transport occurs downward and therefore can take advantage of gravity (particularly at night). However, during the day, phloem transport must occur against the tree water potential gradient, which is generated by the transpiration stream in the xylem. Phloem transport should therefore be strongly coupled to whole plant water relations, i.e., xylem water potential and its gradient. Detailed modeling studies (Ferrier et al. 1975; Thompson and Holbrook 2003; Hölttä et al. 2006) demonstrate this, as does inference from our example calculation by modifying the water potential term in Eq. 2.2. There is also accumulating experimental evidence showing decreased phloem turgor pressures and exudation rates in connection with more negative xylem water potentials (e.g., Cernusak et al. 2009).

The impairments in phloem transport have also recently been raised as one candidate that may affect tree function, and even survival, during drought (McDowell and Sevanto 2010; Sala et al. 2010). For example, drought has been shown to decrease the export of sugars from the leaves and to decouple photosynthetic production from below-ground processes (e.g., Ruehr et al. 2009). From a

theoretical point of view, the turgor pressure has to decrease and/or the osmotic concentration to increase due to the decrease in xylem water potential during drought (see Eq. 2.2). A decrease in the turgor pressure gradient clearly slows down phloem transport. Sugars also need to accumulate in the phloem as water potential decreases to prevent an excessive loss of turgor in the phloem. In our earlier example calculation, the total phloem sugar pool consists of approximately 1 week's worth of photosynthesized sugars (total amount of sugars in the phloem divided by the photosynthesis rate). If whole plant water potential decreases by half, the amount of sugars in the phloem must double to maintain a constant turgor pressure (see Eq. 2.2). This requires 1 week's worth of photosynthesis, which is taken away from active metabolic processes and/or must be found in some storage compartment. Another issue with low xylem water potential could be the increase in phloem sap viscosity with increasing sugar concentrations. Sucrose is the main constituent of sugars transported in the phloem, and sap viscosity is an exponentially rising function of sucrose concentration. Highly concentrated solutions become too viscous to be transported efficiently (e.g., Hölttä et al. 2009). This problem could perhaps be partly alleviated by the use of other osmotic substances, such as potassium, to create the turgor pressure required for turgor maintenance and transport without an increase in viscosity. However, in contrast to sucrose, large stores of potassium may not be available.

Also xylem functionality has been found to be dependent on phloem function. Xylem embolism refilling has been shown to require the integrity of phloem transport. Embolism refilling does not occur below a point of phloem girdling (e.g., Salleo et al. 2004). Xylem transport capacity also seems to be dependent on the recycling of ions from the phloem. Xylem sap ionic concentration apparently modifies the hydration state, and therefore the conductivity, of the xylem inter-conduit pit membranes (Zwieniecki et al. 2001). In addition, phloem sap flow also creates a flow in the xylem, so called Münch counterflow, which could be important in driving the transport of, for example, nutrients in the xylem in the absence of transpiration.

2.4 Measuring Phloem Transport

In contrast to the dead, hollow water conducting tissue in the xylem, the phloem consists of living sieve cell complexes, made up of companion cells and sieve tubes (themselves made up of sieve elements). It is very difficult to measure phloem flow and pressure gradients non-intrusively. The living phloem tissue responds strongly to disturbances which has made its function difficult to study *in vivo* (Van Bell 2003). Phloem tubes are under high pressure and defensive mechanisms readily seal off any wounded sieve elements to prevent phloem leaking, for example, after a puncture or an injury. This makes the anatomical and physiological analysis of cut samples difficult and potentially unreliable.

Phloem transport has been measured using radioisotopes, stable isotopes and nuclear magnetic resonance imaging. Findings from isotopic studies suggest that sugars are transported quite directly from photosynthesis to the phloem as the isotopic ratio of phloem sugars has been found to lag behind the isotopic ratio of photosynthetic products by only a short time (Keitel et al. 2003; Gessler et al. 2008). Nuclear magnetic resonance imaging has provided the possibility to monitor the phloem sap flow velocities under laboratory conditions (Windt et al. 2006). Recently, direct measurements of the phloem turgor pressure and its gradient have been obtained by pressure probes glued to exuding stylets of aphids (Gould et al. 2005). Jensen et al. (2011) developed an ingenious system to detect phloem sap velocity based on the use of an aqueous solution of 5(6)-carboxyfluorescein, which is placed on the surface of a gently abraded leaf surface. Once absorbed, the movement of this substance into the plant is followed by shining a low-intensity laser beam on the leaf petiole and following the movement of the front of the photo-bleached fluorescing dye using coupled highly sensitive photodiodes (Schulz 1992).

A potential candidate to measure phloem function non-intrusively under field conditions is stem diameter change measurements. The diameter of both the xylem and the inner bark vary in response to changes in pressure, as any elastic material does respond. Both the xylem and the inner bark diameter change mainly in response to changes in xylem water potential due to transpiration, but one would also expect that stem diameter changes also responded to changes in phloem sugar dynamics (Sevanto et al. 2003; DeSchepper and Steppe 2010). However, no theoretical framework has yet been presented to obtain phloem flow dynamics from stem diameter change measurements.

2.5 Assimilate Production and Phloem Transport

Assimilate transport from leaves and utilization at sugar sinks are necessary requirements to maintain continuous photosynthetic production in the leaves. Without sufficient transport capacity, the storage capacity of the leaves would eventually become exhausted. Sugar and starch accumulation in the leaves will cause stomatal gas exchange to be limited and photosynthesis to be down-regulated (e.g., Goldschmidt and Huber 1992; Paul and Foyer 2001). This has been shown to occur for example in response to elevated CO₂ concentrations and phloem girdling.

Similarly, as stomatal conductance efficiently controls the leaf gas exchange (Cowan and Farquhar 1977), especially to avoid dangerous levels of xylem embolism, it could also simultaneously control efficient assimilate transport in the leaf phloem. Due to xylem-phloem linkages, insufficient stomatal control could lead not only to xylem cavitation but also to a reverse flow in the phloem, sugar accumulation in the leaves, and to a loss of turgor pressure elsewhere in the phloem transport pathway (Hölttä et al. 2006). The water potential gradient controlling xylem flow and affecting phloem flow is created at the leaf tissue where

transpiration creates the hydrostatic pull lifting water up from soil through xylem. Similarly, photosynthesis and sugar phloem loading in leaves facilitate moving assimilates down the phloem. Depending on the degree of stomatal opening and the prevailing environmental conditions, the relationships between these driving gradients, xylem water transport and assimilate transport from the leaves change.

Acknowledgments T. Hölttä received funding from Academy of Finland project #1132561. M. Mencuccini received funding from NERC grant number NE/I011749/1.

References

- Cernusak LA, Arthur DJ, Pate JS, Farquhar GD (2009) Water relations link carbon and oxygen isotope discrimination to phloem sap sugar concentration in *Eucalyptus globulus*. *Plant Physiol* 131:1544–1554
- Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment. *Symp Soc Exp Biol* 31:471–505
- DeSchepper V, Steppe K (2010) Development and verification of a water and sugar transport model using measured stem diameter variations. *J Exp Bot* 61:2083–2099
- Ferrier JM, Tyree MT, Christy AL (1975) The theoretical time-dependent behavior of a Münch pressure-flow system: the effect of sinusoidal time variation in sucrose loading and water potential. *Can J Bot* 53:1120–1127
- Gessler A, Tcherkez G, Peuke AD, Ghashghaie J, Farquhar GD (2008) Experimental evidence for diel variations of the carbon isotope composition in leaf, stem and phloem sap organic matter in *Ricinus communis*. *Plant Cell Environ* 31:941–953
- Goldschmidt EE, Huber SC (1992) Regulation of photosynthesis by end-product accumulation in leaves of plants storing starch, sucrose and hexose sugars. *Plant Physiol* 99:1443–1448
- Gould N, Thorpe MR, Koroleva O, Minchin PEH (2005) Phloem hydrostatic pressure relates to solute loading rate: a direct test of the Münch hypothesis. *Funct Plant Biol* 32:1019–1026
- Hölttä T, Vesala T, Sevanto S, Perämäki M, Nikinmaa E (2006) Modeling xylem and phloem water flows in trees according to cohesion theory and Münch hypothesis. *Trees* 20:67–78
- Hölttä T, Mencuccini M, Nikinmaa E (2009) Linking phloem function to structure: analysis with a coupled xylem–phloem transport model. *J Theor Biol* 259:325–337
- Jensen KH, Lee J, Bohr T, Bruus H (2010) Osmotically driven flows in microchannels separated by a semipermeable membrane. *J Fluid Mech* 636:371–396
- Jensen KH, Lee J, Bohr T, Bruus H, Holbrook NM, Zwieniecki MA (2011) Optimality of the Münch mechanism for translocation of sugars in plants. *J R Soc Interface*. doi:10.1098/rsif.2010.0578
- Keitel C, Adams MA, Holst T, Matzerakis A, Mayer H, Rennenberg H, Gessler A (2003) Carbon and oxygen isotope composition of organic compounds in the phloem sap provides a short term measure for stomatal conductance of European beech (*Fagus sylvatica* L.). *Plant Cell Environ* 26:931–936
- Knoblauch M, Peters WS (2010) Münch, morphology, microfluidics – our structural problem with the phloem. *Plant Cell Environ* 33:439–452
- Lang A (1979) A relay mechanism for phloem translocation. *Ann Bot* 44:141–145
- McDowell NG, Sevanto S (2010) The mechanisms of carbon starvation: how, when, or does it even occur at all? *New Phytol* 186(2):264–266
- McQueen JC, Minchin PEH, Thorpe MR, Silvester WB (2005) Short-term storage of carbohydrate in stem tissue of apple (*Malus domestica*), a woody perennial: evidence for involvement of the apoplast. *Funct Plant Biol* 32:1027–1031

- Mencuccini M, Hölttä T (2010) The significance of phloem transport for the speed of link between canopy photosynthesis and belowground respiration. *New Phytol* 185:189–203
- Mencuccini M, Hölttä T, Martinez-Vilalta J (2010) Design criteria for models of the transport systems of tall trees. In: Meinzer FC, Dawson T, Lachenbruch B (eds) Size- and age-related changes in tree structure and function. Springer tree physiology series. Springer-Verlag, New York (in press)
- Minchin PEH, Thorpe MR (1987) Measurement of unloading and reloading of photoassimilate within the stem of bean. *J Exp Bot* 38:211–220
- Mullendore DL, Windt CW, Van As H, Knoblauch M (2010) Sieve tube geometry in relation to phloem flow. *Plant Cell* 22:579–593
- Paul MJ, Foyer CH (2001) Sink regulation of photosynthesis. *J Exp Bot* 52:1383–1400
- Peuke AD, Windt CW, Van As H (2006) Effects of cold girdling on flows in the transport phloem in *Ricinus communis*: is mass flow inhibited? *Plant Cell Environ* 29:15–25
- Quilhó T, Pereira H, Richter HG (2000) Within-tree variation in phloem cell dimensions and proportions in *Eucalyptus globulus*. *IAWA J* 21:31–40
- Ruehr NK, Offermann CA, Gessler A, Winkler JB, Ferrio JP, Buchmann N, Barnard RL (2009) Drought effects on allocation of recent carbon: from beech leaves to soil CO₂ efflux. *New Phytol* 184:950–961
- Sala A, Piper F, Hoch G (2010) Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytol* 186:274–281
- Salleo S, LoGullo M, Trifilò P, Nardini A (2004) New evidence for a role of vessel-associated cells and phloem in the rapid xylem refilling of cavitated stems of *Laurus nobilis*. *Plant Cell Environ* 27:1065–1076
- Schulz A (1992) Living sieve cells of conifers as visualized by confocal, laser-scanning fluorescence microscopy. *Protoplasma* 166:153–164
- Sevanto S, Vesala T, Perämäki M, Nikinmaa E (2003) Sugar transport together with environmental conditions controls time lags between xylem and stem diameter changes. *Plant Cell Environ* 26:1257–1265
- Thompson MV (2006) Phloem: the long and the short of it. *Trends Plant Sci* 11:26–32
- Thompson MV, Holbrook NM (2003) Scaling phloem transport: water potential equilibrium and osmoregulatory flow. *Plant Cell Environ* 26:1561–1577
- Thorpe MR, Furch ACU, Minchin PEH, Föller J, Van Bell AJE, Hafke JB (2010) Rapid cooling triggers forisome dispersion just before phloem transport stops. *Plant Cell Environ* 33:259–271
- Turgeon R (2010) The puzzle of phloem pressure. *Plant Physiol* 154:578–581
- Van Bell AJE (2003) The phloem, a miracle of ingenuity. *Plant Cell Environ* 26:125–149
- West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. *Nature* 400:664–667
- Windt CW, Vergeldt FJ, de Jager PA, Van As H (2006) MRI of long-distance water transport: a comparison of the phloem and xylem flow characteristics and dynamics in poplar, castor bean, tomato, and tobacco. *Plant Cell Environ* 29:1715–1729
- Zwieniecki MA, Melcher PJ, Holbrook NM (2001) Hydrogel control of xylem hydraulic resistance in plants. *Science* 291:1059–1062

Trees in a Changing Environment

Ecophysiology, Adaptation, and Future Survival

Tausz, M.; Grulke, N. (Eds.)

2014, XII, 287 p. 54 illus., 13 illus. in color., Hardcover

ISBN: 978-94-017-9099-4