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Current Opinion in Plant Biology

Phloem physics: mechanisms, constraints, and perspectives

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Plants have evolved specialized vascular tissues for the distribution of energy, water, nutrients, and for communication. The phloem transports sugars from photosynthetic source regions (e.g. mature leaves) to sugar sinks (e.g. developing tissues such as buds, flowers, roots). Moreover, chemical signals such as hormones, RNAs and proteins also move in the phloem. Basic physical processes strongly limit phloem anatomy and function. This paper provides an overview of recent research and perspectives on phloem biomechanics and the physical constraints relevant to sugar transport in plants.

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Current Opinion in Plant Biology 2018, **43**:96–100

This review comes from a themed issue on **Physiology and metabolism**

Edited by **Noel Michele Holbrook** and **Michael Knoblauch**

https://doi.org/10.1016/j.pbi.2018.03.005

Introduction

Plants are uniquely decentralized organisms. They communicate, transport matter over great distances, and perceive injury in a complex distribution network without mechanical pumps, nerves or a brain [1,2,3••,4]. To provide these complex functions, they integrate basic physical mechanisms at the cellular level, such as osmosis, diffusion, fluid flow, and elastic processes.

Photosynthesis in plant leaves converts light energy into chemical energy which is stored in sugar molecules for later use in metabolism and growth [1,2]. Sugars are exported from the leaf by bulk liquid flow through the phloem vasculature. This tissue forms a complex distribution system responsible for integral functions in vascular plants, however, surprisingly little is known of its biophysics and biomechanics. The inaccessibility of the tissue and difficulties in imaging and automating the process of discriminating of between sieve elements and other cell types makes the task of quantifying transport and mapping the conductive system difficult [3••]. In contrast to animals, the physical design parameters (e.g. transport efficiency, resilience to damage and fluctuations in supply, or growth patterns) which influence the network architecture thus remain poorly understood [4].

Long-distance transport by pressure-driven flow

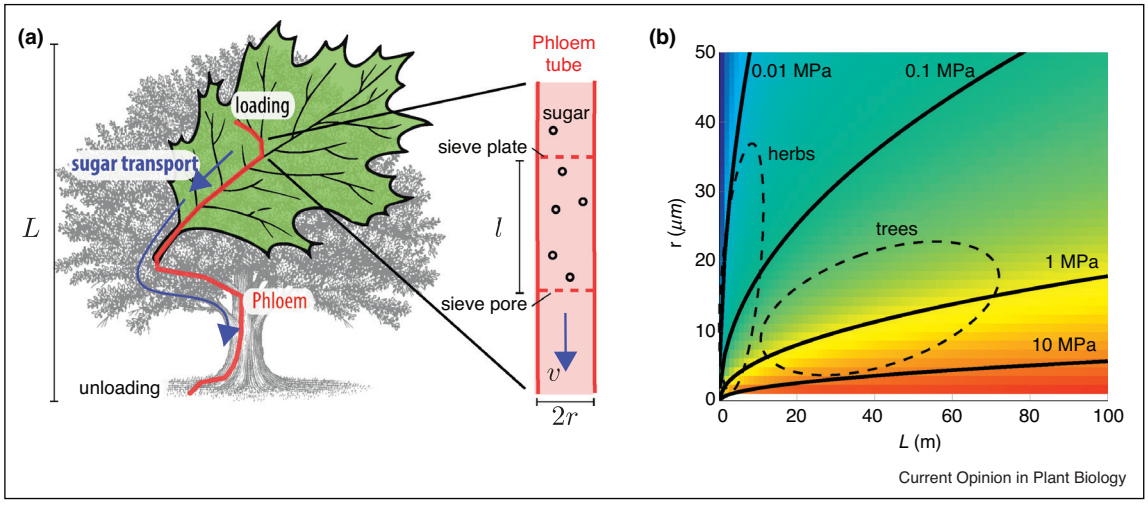
Phloem tubes form a microfluidic network linking distal parts of vascular plants (Figure 1(a)). The conductive cells are approximately cylindrical, of radius $r = 1 - 50$ μm and length $l = 100 - 1000$ μm (see Table 1 for a complete list of symbols). Cellular conduits are connected end-to-end (and in some cases radially) by sieve plates, modified cell wall perforated by numerous enlarged plasmodesmata (PD) pores of radius $r_p = 0.1 - 1$ μm [2]. The phloem conduits carry a sap which contains ~20% sugar by weight [5], and the average flow speeds are in the range of $v = 25 - 250$ μm/s (ca. 0.1–1 m/h), resulting in laminar low-Reynolds-number flow conditions dominated by viscous effects [2,6].

Plants are among the largest and most morphologically diverse organisms [7] and source and sink regions can be separated by distances of up to approximately $L = 100$ m. Overcoming resistance to flow in the phloem consequently requires substantial pressure differences between sources and sinks. To a first approximation, the pressure required to drive flow is given by the Hagen–Poiseuille (or Darcy's) law, which relates pressure difference Δp and flow rate Q and flow speed $v = Q/\pi r^2$:

$$\Delta p = \frac{8\eta L}{\pi r^4} S_p Q = 8\frac{\eta L}{r^2} S_p v. \quad (1)$$

Here, $\eta \simeq 2$ m Pa s is the sap viscosity and L is the total transport distance. The sieve-plate-factor $S_p = 2$ quantifies the resistance to flow through sieve pores, which approximately doubles the pressure [8]. Typical pressures relevant to phloem transport are illustrated as function of conduit radius and plant size in Figure 1(b). It is apparent that relatively large forces are required; typically pressures of several MPa in large plants. This is significantly greater than, for example, human blood pressure (~0.01 MPa), and the link between pressure and geometry imposes strong constraints on transport efficiency because the energetic cost of sugar transport due to viscous dissipation scales with the pressure [2].

Figure 1



(a) Phloem tubes form a microfluidic network responsible for sugar transport in plants. The conductive cells are approximately cylindrical of radius *r* and length *l*. Perforated sieve plates connect adjacent vascular elements. **(b)** Surface plot showing the pressure difference Δp required to drive phloem transport in channels of radius *r* over a transport distance *L* at a speed of $v = 100\,\mu m/s$ computed from Eq. [1]. Colors illustrate the magnitude of the pressures ranging from relatively small (blue) to large (red), and curves of constant pressure drop are highlighted by solid lines. Regions delimited by dashed lines highlight typical single-point observations of phloem dimensions in herbs and trees. Data from [37].

The motile force responsible for generating phloem pressure flow (Eq. [1]) is believed to be osmosis: According to the Münch hypothesis, sugars accumulating in photosynthetic regions lead to an osmotic increase in cell turgor pressure [1]. By contrast, unloading in sink regions lowers the pressure. This provides a difference in pressure of $\Delta p = \Delta\Psi + RT\Delta c$, where $\Delta\Psi$ is the gradient in external water potential, R is the gas constant, T is absolute temperature, and Δc is the available source-to-sink difference in concentration. The magnitude of Δc is influenced by the loading and unloading mechanisms and the concentrations of background non-saccharide osmotica [1]. A concentration difference of $\Delta c = 0.5$ M leads to an available pressure of approximately 1 MPa, which is sufficient to drive transport in small plants. However, the feasibility of pressure-driven flow in tall trees has been questioned on the basis of generating sufficient pressures and transport rates, and alternative mechanism proposed (reviewed in [9]).

Table 1

List of symbols

Symbol	Description	Unit
A	PD conductive area	m^2
c	Concentration	mol/m^3
Δc	Concentration difference	mol/m^3
D	Diffusion coefficient	m^2/s
d	PD length	m
I	Loading rate	mol/s
k	PD permeability	m^2
L	Phloem transport distance	m
l	Sieve tube length	m
Δp	Pressure difference	Pa
Q	Phloem sap flow rate	m^3/s
R	Gas constant	J/(K mol)
r	Sieve tube radius	m
r_p	Sieve pore radius	m
S_p	Sieve plate resistance factor	–
T	Temperature	K
v	Velocity	m/s
η	Viscosity	Pa s

Recent studies have highlighted that (i) the source-to-sink pressure difference increases with organism size L [10], and (ii) the phloem radius varies along the plant axis, generally increasing from the smallest conduits in the leaf phloem to larger tubes in the stem [11]. This supports the feasibility of Münch-pressure-flow as the mechanism of phloem transport in vascular plants. However, the concept has yet to be tested in a large set of species, and widely applicable experimental methods are not yet in place. Moreover, recent works have highlighted striking differences in leaf phloem architecture between, for example, *Gingko* [12••], *Populus* [13••], and pine needles [14]. Poplar phloem follows the da Vinci-rule, where the cross-sectional area of conductive phloem at a given branching order is equal to the sum of the cross-sectional areas of the next highest order of branching. By contrast, the conductive area in pine needles scales with distance from the tip in a different manner in order to minimize the pressure drop required to drive transport, while *Ginko* follows neither principle. The cues which facilitate spatially coordinated changes in phloem development and

osmotic potentials are unknown. However, it is apparent that the common linear-pipe approach to phloem modeling may be insufficient [15••], and that a general temporally and spatially resolved model of the phloem as a poroelastic material is required.

Phloem loading

A critical feature of long-distance vascular transport is an efficient mechanism for loading of cargo. In plants, the products of photosynthesis are loaded by transferring sugar molecules from photosynthetic cells (mesophyll) to the phloem vasculature. Loading is important: photosynthesis is down-regulated and plant productivity is reduced if loading cannot keep up with production [16]. Moreover, the available pressure to drive vascular flow is directly related to the phloem sugar content because the osmotic pressure of the sap provides the necessary force to drive bulk flow out of the leaf [2].

Plants use a range of mechanism to load sugars [17•]. Many species transfer sugars into the phloem by using energy-consuming processes such as membrane transporters (active apoplastic loading) or enzymatic polymerization of sugars (active symplastic loading). In the latter 'polymer-trap mechanism', sugars first diffuse from the mesophyll into phloem cells through PD pores. Here, sucrose is converted into larger sugar polymers, raffinose and stachyose, and is thus segregated (trapped), because they become too large to diffuse back into the mesophyll cells through the PD. For details of the kinetics of this transport mechanism, see [18,19]. Active apoplastic loading is the dominant mechanism in herbaceous plants, while the polymer-trap mechanism occurs in a few families (e.g. cucurbits) [17•]. Both these active/enzymatic strategies have the distinct advantage that the sugar content of the phloem can exceed the mesophyll, that is, $c_p > c_m$. Interestingly, many large trees appear to rely on a phloem loading mechanism which is driven purely by thermal/entropic effects: sugars first diffuse into the phloem via plasmodesmata channels and are subsequently pumped out of the leaf by osmosis [17•,20]. In contrast to active loading processes, this 'symplastic passive loading' mechanism requires no external energy input beyond the gradient in chemical potential provided by the local synthesis and distal consumption of sugars. In symplastic passive loading, the diffusive loading rate I can be expressed as

$$I = \frac{AD(c_m - c_p)}{d} \tag{2}$$

where A is the combined area of all pores, d is the pore length, D is the effective diffusion coefficient of the PDs, and the factor $c_m - c_p$ is the down-hill concentration gradient from mesophyll to phloem. In diffusive loaders, the sugar concentration in the phloem lower than in the mesophyll. This is extremely surprising, since tall trees would appear to require the largest phloem pressures of all plants to sustain sugar export, because transport resistance is large in trees. This paradox has generated substantial controversy because of the perceived inefficiency of passive loading [21].

Recent experiments on biomimetic devices have demonstrated that diffusive loading is feasible [22]. However, the experiments also revealed that it most useful in the very tallest category of trees, because a large resistance to flow in the stem phloem is required for the osmotic pumping mechanism to operate effectively: The maximum driving force and sugar output for any passive loader is achieved when the phloem sugar concentration is equal to the mesophyll sugar content. This occurs when the resistance to flow in the stem is relatively large, that is, in tall trees, and intermediate size trees may require a different loading strategy.

To resolve the question of passive phloem loading and its feasibility in moderate size trees, it was recently proposed that bulk flow through plasmodesmata may provide an additional minor path for loading (e.g. [18,19,23•]). PDs are most often associated with diffusive transport processes, and previous experiments have focused on testing the diffusive connectivity of leaf cells by tracing cell-to-cell transport of fluorescent molecules (e.g. [24•]). However, plasmodesmata are functionally similar to gap junctions (pores that link animal cells) which allow for bulk flow of water [25]. To quantify the relative importance of diffusion and advection (c.f. Eq. [2]), a global model of coupled water fluxed inside of the leaf should be considered. If we, for simplicity consider only the mesophyll-to-phloem coupling, the loading rate I can be written as the sum of the two effects:

$$\begin{aligned} I &= \text{DIFFUSION} + \text{ADVECTION} \\ &= \frac{AD(c_m - c_p)}{d} + \frac{Ak\Delta p}{d}\frac{c_m}{\eta(c_m)} \end{aligned} \tag{3}$$

where k is the hydraulic permeability of the plasmodesmata pores, $\eta(c_m)$ is the concentration-dependent sap viscosity, and $\Delta p = RT(c_m - c_p)$ is the osmotic pressure difference between mesophyll and phloem. Here, R is the gas constant and T is temperature. The relative importance of advection and diffusion in the loading process is characterized by the loading Peclet-number

$$Pe = \frac{\text{ADVECTION}}{\text{DIFFUSION}} = \frac{kRT}{D}\frac{c_m}{\eta(c_m)} \tag{4}$$

Using parameter estimates from the literature ($k = 1 - 10 \times 10^{-18}$ m^2, $RTc_m = 0.5$ MPa, $D = 5 \times 10^{-10}$m^2/s, $\eta(c_m) = 2$ m Pa s) [2], we observe that Pe varies in the range

~0.5–5. This implies that bulk flow might play a significant role in passive loading. The structure of Eq. [2] also suggest that while a large mesophyll sugar concentrations c_m is generally favorable, the ratio of concentration to viscosity $c_m/\eta(c_m)$, and hence advective loading rate, peaks near $c_m \simeq 20\%$ wt. This suggests a possible rational for the surprisingly uniform sugar concentration in passive loaders, which has been attributed to minimizing the energetic cost of long-distance phloem transport [5].

Phloem unloading

In plants, the products of photosynthesis in green tissues are delivered by the phloem to distant organs where they are utilized in growth, metabolism, or storage. Moreover, the solvent carrier (water) leaves the phloem and contributes to growth or is recirculated in the xylem [1]. The process by which solutes exit the phloem is termed phloem unloading, and is a key mechanism for regulating the flux of carbon into sink tissues [26].

A number of potential unloading mechanisms have been identified, and as in phloem loading they involve a combination of energized membrane transporters and passive processes in PD pores [27]. In PD-mediated unloading the pores facilitate a combination of diffusive and advective transport of sugars out of the phloem, into specialized cells. Numerous and large plasmodesmata clearly provide the most efficient pathway for unloading. However, the pores should not be too large: this can lead to movement of viruses and bacteria and leakage of valuable cell components. On the other hand, the pores cannot be too small: This would quickly lead to clogging in sink tissue by the abundant macromolecules which are trafficked in the phloem. The physical design principles of unloading PDs is unclear, but it may have properties similar to other natural nano-pores [28]. A striking feature of unloading PDs is that they are pressure-sensitive: when the pressure difference between phloem and target cells is small, sugars are released continually until the pores are clogged by a plug of macromolecules [29]. This leads to a built-up of pressure in the phloem and the plug is pushed through the PD. The physical gating mechanism responsible for this effect remains unknown, but elastic deformations of the cell wall may influence transport [30•]. We note that similar pressure-sensitive PDs have been observed in leaf trichomes [31••].

Perspectives

The phloem remains one of the most important yet least understood plant tissues. As outlined in this paper, key questions remain regarding the physical feasibility of central processes that facilitate the loading, transport, and unloading of cargo in the complex network formed by phloem cells. Moreover, the mechanical processes that are involved in wound response [32] and signal transmission [33,34], and the network's response to damage and fluctuations in supply/demand [15••,35] in the phloem are not well understood.

Finally, we highlight the importance of understanding the physical processes involved in the spreading of pathogens in the phloem. Pathogens pose minor threats when infecting single cells or spreading within a single leaf. But once the pathogen enters the phloem, systemic infection and a resulting major loss in productivity are unavoidable. Phloem-mobile viruses and bacteria cause epidemics in all agronomically important crops, and resulting yield losses range between 20% and 40% worldwide [36].

Acknowledgements

This work was supported by a research grant (13166) from VILLUM FONDEN.

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