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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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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

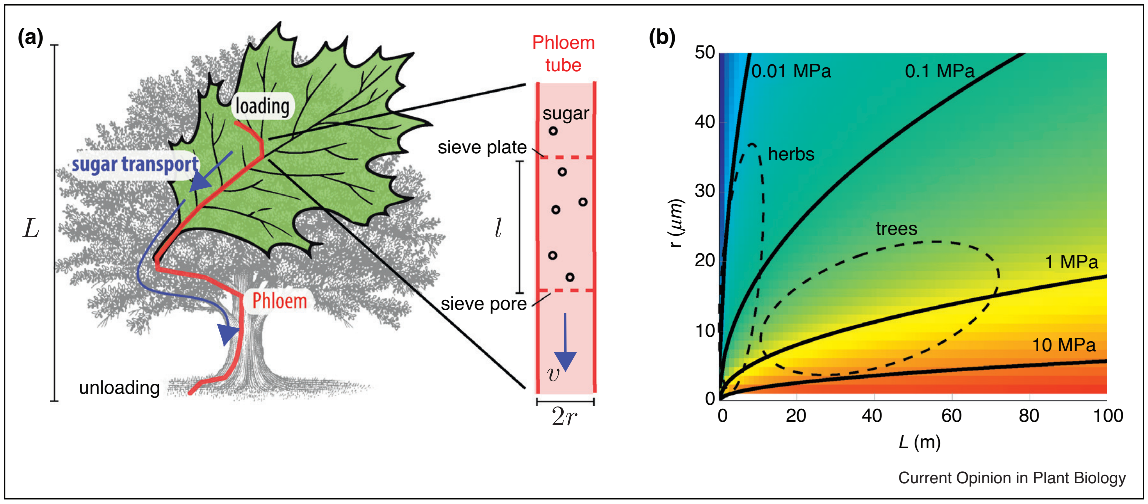
Phloem tubes form a microfluidic network linking distal parts of vascular plants (Figure 1(a)). The conductive cells are approximately cylindrical, of radius $r = 1 - 50$ μm and length $l = 100 - 1000$ μm (see Table 1 for a complete list of symbols). Cellular conduits are connected end-to-end (and in 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 $v = Q/\pi r^2$:

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

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 $v = 100\ \mu\text{m/s}$ 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