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# Editorial overview: Physiology and metabolism: Phloem: a supracellular highway for the transport of sugars, signals, and pathogens

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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.2018.05.013>

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## N Michele Holbrook and Michael Knoblauch

**N Michele Holbrook** is Charles Bullard Professor of Forestry in the Department of Organismic and Evolutionary Biology at Harvard University. Her research focuses on the physics and physiology of vascular transport in plants with the goal of understanding how constraints on the movement of water and solutes between soil and leaves influences ecological and evolutionary processes. An on-going collaboration with Michael Knoblauch demonstrates that Münch flow can account for carbohydrate transport in long vines and tall trees. Recent research focuses on how transpiration-induced water potentials affect the export of carbohydrates from leaves.

**Michael Knoblauch** is Professor of Plant Cell Biology in the School of Biological Sciences and Director of the Franceschi Microscopy and Imaging Center at Washington State University. His research group investigates cell biological phenomena that have an impact on whole plant physiology and ultimately on food security, climate change and bioenergy crops. Their focus is on sieve elements and in utilizing molecular biological-, cell biological-, and bio-imaging tools and develop new methods and protocols to enable previously impossible studies, including in vivo measurements of sieve tube turgor pressure and hydraulic characterization of sieve plates. Recent studies focus on phloem unloading, sieve tube proteomics, long distance signaling and plant pest interactions.

The phloem plays a central role in the functioning of plants [1,2]. As the nexus for carbohydrate distribution within plants, this network of living conduits sits at the epicenter of the mechanisms that control allocation of resources between sources and sinks. Thus, the agronomic and ecological implications of understanding phloem functioning are huge. Nearly all of the food that we eat and all of the carbon sequestered by forests is translocated through the phloem.

Furthermore, the phloem is much more than a system for distributing resources. Phloem contributes to whole plant integration by transporting information and ‘perceiving’ injury. At the same time, the phloem makes plants vulnerable to pathogens, which use it as a pathway for infection. Phloem-mobile viruses and bacteria cause epidemics in all agronomically important crops, and resulting yield losses range between 20% and 40% worldwide [3].

The present issue highlights recent progress in understanding phloem biology and provides a guidepost for future research. The papers collected here focus on classical issues relating to carbohydrate transport such as how the structure of sieve elements affects the osmotically generated pressure gradients needed to drive flow [4], as well as more recent concerns such as what controls the entry and exit of signaling molecules into the phloem, how the phloem is both used by and protected from biotic vectors, and the extent to which phloem functioning may be impacted by drought and climate change [5]. These issues lie at heart of food production and ecosystem functioning and thus are central to how research on phloem can contribute towards our collective future [6].

### Phloem structure and development

Sieve elements are among the most highly differentiated cells in the plant body. During maturation, they undergo wall remodeling, including the formation of the sieve plate, and the loss of many organelles, notably both the vacuole and the nucleus. Anne and Hardtke [7] review progress in unraveling the genetic network underlying specification of protophloem identify and, in particular, the key role of Octopus gene family as a master regulator of sieve element differentiation.

Several recent studies have focused on how sieve tube structure, and thus hydraulic resistance to flow, varies as a function of position within the plant

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[8–10]. In a review of the biophysics of phloem transport, Jensen [11] highlights how the scaling of sieve tube size and structure affects the pressure gradient needed to drive phloem sap from sources to sinks. This then raises the question of how the architecture of the phloem network arises from the position-dependent differentiation of individual sieve elements. From this perspective, Carvalho *et al.* [12] review new work investigating phloem networks within leaves. They focus on how sieve tube structure varies with vein order, comparing leaves with different venation patterns. One of the advantages of net venation appears to be that the total amount of phloem in minor veins can be huge, and that these loading regions then feeds into a smaller number of larger conduits in larger veins.

At the same time that we have increasing confidence in Münch flow as the mechanism for phloem transport in all angiosperms [9], much about carbohydrate movement in gymnosperms remains mysterious. Not only are gymnosperm sieve cells narrower than in angiosperms, but the structure of sieve area pores is more akin to plasmodesmata than to the open sieve plate pores. Liesche and Schulze [13] review recent work on the structure of gymnosperm phloem. They note that the sieve cells found in gymnosperms are wider at the base of the plant, suggesting that the design principles guiding phloem network architecture are similar between these two major groups of seed plants. In addition, they highlight the question of whether the ER that penetrates sieve area pores in gymnosperms should be seen solely as an obstruction to flow, or whether it may, in fact, have an active role in moving phloem sap from one sieve cell to the next.

### Phloem transport of carbohydrates and other metabolic cargo

Carbohydrate transport is the central task of the sieve tube system. Before phloem loading can occur in leaves, carbohydrates must move from their sites of synthesis in mesophyll cells to the veins. Rockwell *et al.* [14] address how water potential gradients within the leaf due to transpiration affect the pre-phloem movement of sugars and under what circumstances Münch flow (convection) in symplasmic loaders might be said to begin in the mesophyll.

After the cargo moves to the veins, it must then be loaded. Three distinct loading mechanisms have been described [15]. Solutes may follow a concentration gradient from mesophyll cells to sieve tubes, which is reflected in numerous plasmodesmata connecting adjacent cells to provide a symplastic path of low resistance [16]. Other plant species create an apoplasmic barrier to control loading via membrane transporters [17]. The third mechanism involves passive diffusion through plasmodesmata, but a subsequent polymerization of the cargo to increase

its size exclusion limit and prevent back-diffusion [18]. These mechanisms have seen great experimental support over the last decades. Zhang and Turgeon [19] provide a critical review and new perspectives.

Investigations on phloem transport have suffered for a long time from the inaccessibility of the cells. Usually they are deeply embedded in opaque layers of protective dermal, cortical, and sclerenchyma tissue making direct observation difficult. New imaging tools utilizing transparent tissues or preparative protocols to visualize living sieve tubes, together with a palette of newly discovered phloem mobile dyes that use different loading modalities mimicking those of natural compounds allow us now to track loading, transport, and unloading *in situ* are reviewed by Knox and Oparka [20].

Experimental challenges also hold true for the unloading process into sinks, which is a central process in defining allocation. A mature plant usually contains thousands of sinks competing for resources. A central question here is, what defines sink strength? While the initial step of unloading in some sinks such as roots is symplastic via specialized plasmodesmata, post-unloading may involve transporters. In other sinks like developing seeds a mandatory apoplasmic step exists which requires active transport over the membrane. Passive unloading is dominated by biophysics via the conductivity of plasmodesmata and transporters, which are driven by a concentration gradient. Active uptake is controlled by transporters and their expression profile. How a plant controls these mechanisms in order to balance distribution to all sinks is a matter of intense study. Progress in this area is reviewed and discussed by Milne *et al.* [21].

Lee and Frank [22] discuss the specialized plasmodesmatal connections that regulate the entry and exit of material into the phloem, noting that this includes the phloem's metabolic cargo, as well as long-distance signaling molecules and superfluous escapees. They highlight the discovery of structurally distinct 'funnel' plasmodesmata that connect protophloem sieve elements with phloem pole pericycle cells and serve as the major unloading pathway in roots. Carbohydrates are also unloaded and stored in large amounts in stems. Given that 40% of a tree's non-structural carbon stores are located within their stems, Furze *et al.* [23] argue that the phloem needs to be understood as more than a long-distance highway and that a greater focus on the distributed unloading into storage that occurs within stems will provide insights relevant to the growth and allocation patterns of trees.

While carbohydrates usually account for the majority of transported solutes in the phloem, numerous other cargos are present in the phloem sap. Major components of high importance are nitrogen compounds such as amino acids.

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