

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

N Michele Holbrook and Michael Knoblauch



Current Opinion in Plant Biology 2018, 43:iii–vii

For a complete overview see the [Issue](#)

Available online 28th May 2018

<http://dx.doi.org/10.1016/j.pbi.2018.05.013>

1369-5266/© 2018 Elsevier Ltd. All rights reserved.

## N Michele Holbrook

Department of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge, MA 02138, USA  
e-mail: [holbrook@oeb.harvard.edu](mailto:holbrook@oeb.harvard.edu)

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

School of Biological Sciences, Washington State University, PO Box 644236, Pullman, WA 99164-4236, USA  
e-mail: [knoblauch@wsu.edu](mailto:knoblauch@wsu.edu)

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-imaging, cell biological-imaging, 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

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 [8–10]. In a review of the biophysics of phloem transport, Jensen [11]

characterization of sieve plates. Recent studies focus on phloem unloading, sieve tube proteomics, long distance signaling and plant pest interactions.

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 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 apoplastic 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 plasmodesmata 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. While N components can in principle follow the same symplastic route as carbohydrates in passive loaders, specific transporters are required to cross membranes. Recent studies on amino acid transporters have also shown that the notion that photosynthesis is the defining and limiting factor for plant yield, and that all other processes follow if only we would be able to increase photosynthesis capacity, is short sighted. Overexpression of transporters (e.g. AtAAP1) in sinks may lead to significant increases in yield and upregulation of photosynthesis. [Tegeger and Hammes \[24\]](#) discuss the processes of N phloem loading, unloading and the impact of manipulations of transporter expression levels, while the issue of source or sink limitation and next generation strategies for crop yield improvement are the focus of the paper by [Sonnewald and Fernie \[25\]](#).

### Phloem as a long-distance highway for the movement of signals and disease vectors

The topic of long distance signaling is currently probably the most controversial topic in phloem biology. A surprising number of molecules, including thousands of proteins and RNAs have been detected in phloem sap but for only a minute fraction of those, a function could be assigned (e.g. flowering locus T). There are different opinions on the impact, the origin and the function of trace components in the phloem sap and our aim was to provide various points of view.

Phloem proteomics has been done so far on phloem exudates, because no methods exist to isolate pure sieve tubes. The current state and technical challenges to collect sieve tube exudate proteins and to identify functional proteins are discussed by [De Marco \*et al.\* \[26\]](#). The fact that thousands of proteins can be found in exudates is certainly a surprise, but that a similar amount of transcripts is present in the sieve tube sap and that those transcripts move over graft unions may be even more surprising. [Morris \[27\]](#) critically discusses the selectivity, specificity and the signaling potential of messenger RNAs in the phloem sap in the context of recent findings.

In general it is assumed that components found in the sieve tube sap originate in neighboring companion cells. Another source of origin, however, exists when young sieve elements degrade their organelles, open up their pores and are integrated in the actively transporting sieve tube. In this moment the degraded substances become part of the sieve tube sap and will be collected in exudates. [Knoblauch \*et al.\* \[28\]](#) provide an evaluation of the contribution of those cellular remnants to the overall phloem sap components and critically discuss the impact on our understanding on signaling and sieve tube structure.

Movement of chemical signals in the translocation stream is limited by phloem flow direction and speed. The cable-like construction provides, however, a structural foundation for other mechanisms such as electrical signals which are independent on phloem flow direction and speed, are much faster and are an ideal basis for long distance information transmission. New techniques on investigating these phenomena have improved our understanding significantly over the last years and are summarized by [Hilleary and Gilroy \[29\]](#).

Furthermore, a large number of pathogens utilize the phloem for systemic infection. While local infection of, for example, individual leaves does not represent a major problem for a plant, pathogens become a real threat once they reach the phloem and spread systemically. Hijacking the phloem obviously requires specific interactions, and improvement of our knowledge certainly bears the hope of creating effective counter measures.

Folimonova and Tilsner [30] provide a critical discussion on our current understanding of cellular mechanisms and interactions between plant viruses and their host plants.

### Phloem transport in a changing world

The future holds many things, including rising atmospheric CO<sub>2</sub> concentration, more intense drought, and greater agricultural demand to supply a human population increasing in both numbers and dietary affluence. Given the central role that carbohydrates and their transport plays in the growth and development of plants, understanding phloem is relevant to predicting and improving the stability and productivity of forest and agricultural systems.

Ainsworth and Lemonnier [31] explore a possible link between loading type and the degree of photosynthetic acclimation to elevated CO<sub>2</sub> thought to arise in response to a build-up of carbohydrates in source tissues. They further discuss transgenic strategies to increase yield by targeting carbohydrate management in both sources and sinks. Without a concomitant increase in sink capacity, limitations in carbohydrate export from leaves can cause photosynthesis to be down regulated.

How drought impacts phloem is discussed by Sevanto [32]. Here the key issue is the extent to which phloem transport can persist even after stomata have closed, thus allowing plants access to stored resources. Integrity of the phloem appears to be essential for surviving severe droughts and loss of phloem turgor one of the best predictors of drought-induced mortality.

### Concluding perspective

The papers collected here demonstrate that phloem research has shifted into high gear. In large part, progress has been enabled by development of new tools, both physiological and genetic, and propelled by the potential for discoveries relevant to crop improvement and ecological resilience. At the same time, there is still much to learn [33]. For example, with the exception of mitochondria we do not even know what the other sieve element organelles do [34]. This is in stark contrast to all other major cell types, where the function of organelles is well established. Because phloem allows the highly decentralized plant body to function as an integrated whole, further work in this area will shed light on the key question of how plants coordinate growth and assimilation in distant regions and thus balance investments between producing new sources and new sinks [35].

### References

- Jensen KH, Berg-Sørensen K, Bruus H, Holbrook NM, Liesche J, Schulz A, Zwieniecki MA, Bohr T: **Sap flow and sugar transport in plants.** *Rev Mod Phys* 2016, **88**:035007.
- Raven JA: **The evolution of vascular land plants in relation to supracellular transport processes.** *Adv Bot Res* 1977, **5**:153-219.
- Savary S, Ficke A, Aubertot JN, Hollier C: **Crop losses due to diseases and their implications for global food production losses and food security.** *Food Secur* 2012, **4**:519-537.
- Knoblauch M, Peters WS: **Münch, morphology, microfluidics – our structural problem with the phloem.** *Plant Cell Environ* 2016, **33**:1439-1452.
- Savage JA, Clearwater MJ, Haines DF, Klein T, Mencuccini M, Sevanto S, Turgeon R, Zhang C: **Allocation, stress tolerance and carbon transport in plants: how does phloem physiology affect plant ecology?** *Plant Cell Environ* 2016, **39**:709-725.
- Braun DM, Wang L, Ruan Y-L: **Understanding and manipulating sucrose phloem loading, unloading, metabolism, and signalling to enhance crop yield and food security.** *J Exp Bot* 2014, **65**:1713-1735.
- Anne P, Hardtke CS: **Phloem function and development – biophysics meets genetics.** *Curr Opin Plant Biol* 2018, **43**:22-28.
- Liesche J, Pace MR, Xu Q, Li Y, Chen S: **Height-related scaling of phloem anatomy and the evolution of sieve element end wall types in woody plants.** *New Phytol* 2017, **214**:245-256.
- Knoblauch M, Knoblauch J, Mullendore DL, Savage JA, Babst BA, Beecher SD, Dodgen AC, Jensen KH, Holbrook NM: **Testing the Münch hypothesis of long distance phloem transport in plants.** *Elife* 2016, **5**:e15341.
- Savage JA, Beecher SD, Clerx L, Gersony JT, Knoblauch J, Losada JM, Jensen KH, Knoblauch M, Holbrook NM: **Maintenance of carbohydrate transport in tall trees.** *Nat Plants* 2017, **3**:965-972.
- Jensen KH: **Phloem physics: mechanisms, constraints, and perspectives.** *Curr Opin Plant Biol* 2018, **43**:96-100.
- Carvalho MR, Losada JM, Niklas KJ: **Phloem networks in leaves.** *Curr Opin Plant Biol* 2018, **43**:29-35.
- Liesche J, Schulz A: **Phloem transport in gymnosperms: a question of pressure and resistance.** *Curr Opin Plant Biol* 2018, **43**:36-42.
- Rockwell FE, Gersony JT, Holbrook NM: **Where does Münch flow begin? Sucrose transport in the pre-phloem path.** *Curr Opin Plant Biol* 2018, **43**:101-107.
- Rennie EA, Turgeon R: **A comprehensive picture of phloem loading strategies.** *Proc Natl Acad Sci U S A* 2009, **106**:14162-14167.
- Turgeon R, Medville R: **The absence of phloem loading in willow leaves.** *Proc Natl Acad Sci U S A* 1998, **95**:12055-12060.
- Sauer N: **Molecular physiology of higher plant sucrose transporters.** *FEBS Lett* 2007, **581**:2309-2317.
- Turgeon R, Gowan E: **Phloem loading in *Coleus blumei* in the absence of carrier-mediated uptake of export sugar from the apoplast.** *Plant Physiol* 1990, **94**:1244-1249.
- Zhang C, Turgeon R: **Mechanisms of phloem loading.** *Curr Opin Plant Biol* 2018, **43**:71-75.
- Knox K, Oparka K: **Illuminating the translocation stream.** *Curr Opin Plant Biol* 2018, **43**:113-118.
- Milne RJ, Grof CPL, Patrick JW: **Mechanisms of phloem unloading: shaped by cellular pathways, their conductances and sink function.** *Curr Opin Plant Biol* 2018, **43**:8-15.
- Lee JY, Frank M: **Plasmodesmata in phloem: different gateways for different cargoes.** *Curr Opin Plant Biol* 2018, **43**:119-124.
- Furze ME, Trumbore S, Hartmann H: **Detours on the phloem sugar highway: stem carbon storage and remobilization.** *Curr Opin Plant Biol* 2018, **43**:89-95.
- Tegeger M, Hammes UZ: **The way out and in: phloem loading and unloading of amino acids.** *Curr Opin Plant Biol* 2018, **43**:16-21.

25. Sonnewald U, Fernie AR: **Next-generation strategies for understanding and influencing source–sink relations in crop plants.** *Curr Opin Plant Biol* 2018, **43**:63–70.
26. De Marco F, Le Hir R, Dinant S: **The rendez-vous of mobile sieve-element and abundant companion-cell proteins.** *Curr Opin Plant Biol* 2018, **43**:108–112.
27. Morris RJ: **On the selectivity, specificity and signalling potential of the long-distance movement of messenger RNA.** *Curr Opin Plant Biol* 2018, **43**:1–7.
28. Knoblauch M, Peters WS, Bell K, Ross-Elliott TJ, Oparka KJ: **Sieve-element differentiation and phloem sap contamination.** *Curr Opin Plant Biol* 2018, **43**:43–49.
29. Hilleary R, Gilroy S: **Systemic signaling in response to wounding and pathogens.** *Curr Opin Plant Biol* 2018, **43**:57–62.
30. Folimonova SY, Tilsner J: **Hitchhikers, highway tolls and roadworks: the interactions of plant viruses with the phloem.** *Curr Opin Plant Biol* 2018, **43**:82–88.
31. Ainsworth EA, Lemonnier P: **Phloem function: a key to understanding and manipulating plant responses to rising atmospheric [CO<sub>2</sub>]?** *Curr Opin Plant Biol* 2018, **43**:50–56.
32. Sevanto S: **Drought impacts on phloem transport.** *Curr Opin Plant Biol* 2018, **43**:76–81.
33. Knoblauch M, Oparka KJ: **The structure of the phloem—still more questions than answers.** *Plant J* 2012, **70**:147–156.
34. Froelich DF, Mullendore DM, Jensen KH, Ross-Elliott TJ, Anstead JA, Thompson GA, Pelissier H, Knoblauch M: **Phloem ultrastructure and pressure flow: sieve-element-occlusion-related agglomerations do not affect translocation.** *Plant Cell* 2011, **23**:4428–4445.
35. Ludewig F, Sonnewald U: **Demand for food as driver for plant sink development.** *J Plant Physiol* 2016, **203**:110–115.