Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Plant Biology

Mechanisms of phloem loading

Cankui Zhang[1] and Robert Turgeon[2]

The complex form of higher plants requires continuous, balanced transport of nutrients in the phloem. The initial step of transferring sugars, amino acids, and other materials from photosynthetic cells to the conducting sieve tubes is known as phloem loading. Three phloem loading mechanisms have been described. The first involves release of sucrose into the apoplast and subsequent retrieval by the phloem. The initial release step in this process is now known to be mediated by a new class of transporters, the SWEET proteins. In the other two loading mechanisms, polymer trapping and diffusion, sucrose passes into the phloem through cytoplasmic channels, the plasmodesmata. Recent models have shed additional light on these mechanisms and their ability to sustain the growth of even the tallest trees.

Addresses
[1] Department of Agronomy and Purdue Center for Plant Biology, Purdue University, West Lafayette, IN 49707, USA
[2] Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, USA

Corresponding author: Turgeon, Robert (ert2@cornell.edu)

Current Opinion in Plant Biology 2018, **43**:71–75

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.2018.01.009

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

Introduction

Phloem transport of nutrients begins with loading sucrose, amino acids and other essential nutrients into the long-distance transport system, composed of the conducting sieve elements (SEs) and their associated companion cells (CCs). The two together form a complex (SE/CC). Most loading occurs in leaves but is not restricted to this site since there is continuous transfer of ions and compounds all along the transport route in response to availability and need. Nevertheless, almost all phloem loading studies focus on leaf structure and physiology.

The analysis of loading mechanisms, and measurements of the amount of nutrient transferred into the transport tissue, is difficult given that the distances are short and the molecules in question highly soluble. A number of experimental strategies have been used, but the challenges are still daunting. In addition, there is a problematic tendency to oversimplify the mechanisms and structures involved, with the result that a given species is often identified as using one loading strategy or another throughout the entire life cycle, and in all environmental conditions, when the reality is undoubtedly more complex. Indeed, heterogeneity in phloem cell differentiation and function is readily apparent in many species [1].

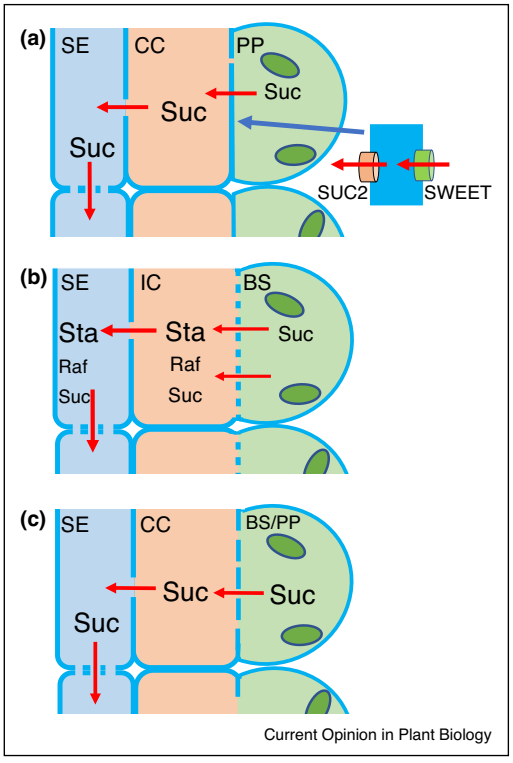
Much present experimentation and discussion revolves around discriminating between two transport pathways: one through the cell wall space between the plasma membranes of two adjoining cells (the apoplast route), and other though plasmodesmata (the symplastic route) (Figure 1). Several authoritative reviews have been published recently [2–5]. Here, we will provide necessary background but will then concentrate on the considerable amount of information that has been published in the last two years.

Apoplastic loading

In most herbaceous plants, sucrose on its way from mesophyll cells to the phloem passes through the apoplast and is loaded into the phloem against a concentration gradient. Given that most agriculturally important species are herbaceous, it is not surprising that this loading strategy was the first to be described and is the most thoroughly studied. Apoplastic loading as a mechanism is, at least in theory, relatively easy to identify since transporters are needed to efflux sucrose into the cell wall space and to load it from this compartment into the phloem. Downregulation of these proteins, either chemically or genetically, provides an experimental approach to dissecting the loading mechanism.

After sucrose has passed from one mesophyll cell to another and has reached a minor vein it is unloaded into the apoplast. How this unloading occurs was a mystery until the discovery of *S*ugar *W*ill *E*ventually be *E*xported *T*ransporters (SWEETs) [6]. SWEETs carry di-saccharide or mono-saccharide across membranes following the concentration gradient. They were first identified with reference to phloem loading [6,7] but were subsequently found to be involved in many important plant processes. Although a single SWEET protein forms a transport path, the proteins are thought to form oligomers. For example, OsSWEET2b from rice is a homotrimer [8]. Recently, the 2.8-A resolution structure of AtSWEET13, which transports both sucrose and glucose across the plasma

Figure 1



Phloem loading mechanisms. **(a)** Apoplastic phloem loading. Sucrose (Suc) enters the apoplast between phloem parenchyma cells (PP) and companion cells (CC) via SWEET transporters and is carried, against a concentration gradient, into the CC-sieve element (SE) complex by sucrose-H^+ transporters (SUC2). Suc is then transported toward the sinks. **(b)** Polymer trapping involves passage of Suc from bundle sheath cells (BS) into specialized companion cells, known as intermediary cells (IC), through specialized plasmodesmata (shown as gaps in the wall). These plasmodesmata are narrower and more numerous than those at the same interface in passive loading species. Inside the IC the Suc is converted into raffinose (Raf) and stachyose (Sta) with the latter dominant. **(c)** In passive phloem loading, Suc at high concentration in the mesophyll passes into the SE/CC complex down its concentration gradient.

membrane during pollen development, has been reported [9•]. AtSWEET11/12 localize to the plasma membrane of cells inside the vein, probably phloem parenchyma cells. This finding is consistent with anatomical evidence suggesting phloem parenchyma cells to be the primary unloading site [10]. Double mutations of the AtSWEET11/12 genes suppresses phloem transport leading to accumulation of starch in leaves [6].

Sucrose uptake from the apoplast is driven by SUTs (SUcrose Transporters), H^+/sucrose symporters that use the proton gradient across the plasma membrane to load sucrose into cells against a concentration gradient [4,5]. Downregulation of SUT1 transporters results in stunted growth and accumulation of starch in leaves [4]. While these general results have been understood for some time, puzzles remain. In particular, the loading scenario in rice is still incompletely understood. On the basis of ultrastructural evidence indicating symplastic discontinuity into the SE/CC [11] and the presence of a proton pyrophosphatase in veins [12], rice would seem to be a classical apoplastic loading species, as is *Zea mays* [13]. Decreased expression of SUT1 reduces grain-filling capacity in rice but these plants do not show typical symptoms of reduced phloem loading [14]. How rice plants with disrupted *OsSUT1* escape phenotypic abnormalities associated with transport inhibition is unclear, but Julius *et al.* [5] suggest it may be due to the low-light growth conditions used in the original experiments, which minimally tax the loading mechanism(s). This recalls the interesting observation that *Arabidopsis thaliana* plants suffering from homozygous null mutation in *AtSUC2* are able to complete their life cycle when grown in low light [15]. On the basis of all evidence so far obtained, Julius *et al.* [5] concluded that rice phloem loads from the apoplast, as do the other monocots so far examined.

A broad spectrum of amino acids is also exported from leaves in the phloem to provide required nitrogen to sinks [16••,17]. Transporter mediated loading of amino acids into the phloem is a bottleneck in this process [18]. The molecular basis for this transport has been elusive but recently Santiago and Tegeder [16••] demonstrated in arabidopsis that *AMINO ACID PERMEASE8* (*AAP8*) is localized to the plasma membrane of leaf phloem and loading of amino acids is reduced in *aap8* mutants [16••], resulting in reduced sink development and plant growth [19].

The above studies emphasize the fact that environmental conditions must be taken into account when analyzing structural and functional aspects of phloem loading and transport. In different light and temperature conditions, vein density, cell number per vein, transporter capacity, and the cell wall characteristics of 'transfer cells' may be modified to adjust to required flux, depending on the species [20–23].

Transfer cells are defined by the presence of extensive invaginations of the cell wall. Transfer cells occur in many, but not all, species at locations where solute flux is high. In minor veins of apoplastic loaders, phloem parenchyma cells channel sucrose into the interior of the veins where it can be efficiently unloaded and reloaded into the SE/CCs [24]. Phloem parenchyma cells and/or CCs may develop ingrowths, depending on the species. Arabidopsis has both [20]. Recent studies have begun to reveal how transfer cell development is regulated. Based on RNAseq analysis, significant changes in gene transcription were found as epidermal cells of *Vicia faba* cotyledon cells transitioned from having smooth walls to developing transfer cell ingrowths [25]. This occurred in a progressive fashion with each phase of

Download English Version:

https://daneshyari.com/en/article/8380256

Download Persian Version:

https://daneshyari.com/article/8380256

Daneshyari.com