Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Plant Biology

Detours on the phloem sugar highway: stem carbon storage and remobilization

Morgan E Furze[1], Susan Trumbore[2] and Henrik Hartmann[2]

For trees to survive, they must allocate resources between sources and sinks to maintain proper function. The vertical transport pathway in tree stems is essential for carbohydrates and other solutes to move between the canopy and the root system. To date, research and models emphasize the role of tree stems as 'express' sugar highways. However, recent investigations using isotopic markers suggest that there is considerable storage and exchange of phloem-transported sugars with older carbon (C) reserves within the stem. Thus, we suggest that stems play an important role not only in long-distance transport, but also in the regulation of the tree's overall C balance. A quantitative partitioning of stem C inputs among storage and sinks, including tissue growth, respiration, and export to roots, is still lacking. Combining methods to better quantify the dynamics and controls of C storage and remobilization in the stem will help to resolve central questions of allocation and C balance in trees.

Addresses
[1] Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford St, Cambridge, MA 02138, USA
[2] Max-Planck Institute for Biogeochemistry, Hans Knoll Str. 10, 07745 Jena, Germany

Corresponding author: Furze, Morgan E (mfurze@fas.harvard.edu)

Current Opinion in Plant Biology 2018, **43**:89–95

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.2018.02.005

Introduction

Trees are organisms that can live for decades, centuries, and even millennia. This long lifespan increases a tree's risk of encountering stressful conditions where normal functioning is disturbed and metabolism has to rely on stored resources [1]. Because trees are autotrophic organisms, storage of primary metabolites like carbohydrates is particularly important for survival during harsh environmental conditions and stress. Carbohydrates are allocated to various organs and processes operating on timescales ranging from hours to decades, each contributing to the tree's overall carbon (C) balance.

Tree stems are predominantly viewed as the infrastructure that provides mechanical support for the canopy and facilities transport between sources and sinks, but they also store ~40% of a tree's total **nonstructural carbohydrates** (NSCs; Box 1) [2•]. During C transport, there is substantial exchange of C between phloem and parenchyma of the stem [3], but a quantitative understanding of C partitioning between storage, tissue growth, and respiration as well as the underlying regulation of C partitioning is still lacking. Here we emphasize that the stem is itself a major C sink and an important organ for the regulation of the tree's C balance, not merely an 'express' highway for long-distance C transport. We stress the need for process-oriented research that will provide quantitative insights into dynamics and controls of C storage and remobilization in tree stems and along the transport pathway. Without such information, the stem will remain a missing link in whole-tree C balance.

Non-structural carbohydrates in the stem

NSCs exist in basically all components of living vegetative tissues of the plant; they can be found in vacuoles, plastids, and the cytosol of cells, as well as in the apoplast [4•]. Supply and demand of NSCs are often asynchronous and surplus sugars produced in leaves during daytime are stored as starch granules in chloroplasts. During the night, these starch granules are then hydrolyzed to glucose to fuel growth and respiration or exported as sucrose to other plant organs via the phloem [5].

Large amounts of NSCs are stored long-term in amyloplasts of **ray and axial parenchyma** cells. Because secondary growth in woody plants produces new cell layers interspersed with living parenchyma cells every year, the resulting tissues provide storage capacities for different temporal horizons: small branches and fine roots serve as seasonal storage, while large branches, coarse roots, and tree stems are used for decadal storage [6•]. Only the heartwood, comprising the inner part of tree branches and stems, does not contain living cells and therefore cannot remobilize remaining NSCs.

In the stem, NSC concentrations usually decrease across the sapwood towards the sapwood-heartwood transition zone and then remain constant (often at zero concentration in older trees) throughout the heartwood to the pith [7]. However, some studies have observed high levels of

Box 1 Glossary of key terms. Terms are bolded within text upon first mention

Term	Definition
Nonstructural carbohydrates (NSC)	Mainly sugars and starch, the major substrates for primary and secondary plant metabolism; 5-C sugars (i.e. glucose, fructose) function as metabolites and osmoregulators, while disaccharides and oligosaccharides (i.e. sucrose, raffinose) function as transport sugars
Ray and axial parenchyma	Living cells of the secondary xylem and phloem that function in many metabolic processes including NSC storage
Collection phloem	Sieve element-companion cell complex of the minor leaf vein that sucrose is loaded into after its production in the leaf mesophyll
Transport phloem	sieve element-companion cell complex in the major veins, petioles, branches, stems, and roots that transports and redistributes NSCs and other molecules to sinks along the vertical pathway
Release phloem	Sieve element-companion cell complex that unloads sucrose and other molecules into sink cells
Leakage-retrieval mechanism	Process by which NSCs traveling along the leaky transport phloem passively diffuse out and are actively loaded back into companion cells
Radiocarbon signatures	Well-documented changes in the radiocarbon signatures atmospheric carbon dioxide since the testing of atmospheric nuclear weapons in the 1960s provide an estimate for the mean time elapsed since C in NSC pools or plant tissues were fixed from the atmosphere
Lateral storage and remobilization	Lateral flow and accumulation of NSCs in sinks (i.e. parenchyma cells of stem xylem) and subsequent release of stored reserves back into the transport phloem
Apoplastic sensing	Proposed mechanism by which lateral flows are regulated through sensing of apoplastic sucrose concentrations; low apoplastic sucrose concentrations will reduce phloem loading

sugars [8••] and/or starch [9] deep in the xylem. NSC concentrations vary seasonally in the stems of several tree species [10], reflecting the accumulation, utilization, and redistribution of NSCs to buffer changing supply and demand throughout the year.

Whole-tree phloem transport

The Münch theory posits that the flux of carbohydrates from sources to sinks is driven by a hydrostatic pressure gradient in the phloem that causes mass flow of phloem sap along the sieve tubes [11,12•,13•]. The hydrostatic pressure is created by loading of sucrose into companion cells followed by diffusion into sieve tubes of the **collection phloem**. The increase in solute concentration in the sieve tubes decreases phloem water potential and causes inflow of water from surrounding tissues, mainly the xylem. Increasing turgor in the collection phloem of source tissues due to this inflow along with unloading of sucrose and ensuing decreases in turgor in the **release phloem** of sink tissues creates the gradient of hydrostatic pressure that drives phloem flow [14•].

Stems are the linkage between the tree's main photosynthetic source, the canopy, and one of its major heterotrophic sinks, the root system. Secondary growth in stems produces layers of cells each growing season, divided into xylem, which transports mainly water and nutrients from the soil to the canopy and **transport phloem**, which redistributes carbohydrates and other organic and inorganic molecules across tree organs. Xylem water transport is much faster than phloem sap flow and can reach maximum peak velocities ranging from 16 to 45 m hour^{-1} depending on vessel size [15]. However, phloem velocities average between 22 cm hour^{-1} in gymnosperm trees and 56 cm hour^{-1} for angiosperms [16•], making tree stems large highways for both water and sugar transport.

Tree stems are more than just unidirectional 'express' highways

Viewing transport phloem in the tree stem as a simple sugar highway is too simplistic (Figure 1). During the last decades, evidence has accumulated that the transport phloem is not an 'express' highway, but rather a leaky pipe where carbohydrates passively diffuse out and are actively loaded back into companion cells during transport [17]; this has been termed the **leakage-retrieval mechanism**. In bean plants, about 6% of sugars are lost and 3.4% retrieved per centimeter of phloem length [18]. Thus, leakage and retrieval may provide resources locally for maintenance and growth of axial sinks like stem cambium [19].

The inverse flows involved in leakage and retrieval are thought to serve as short term buffers for imbalances between sources and sinks, but can also facilitate exchange of NSCs between the phloem and stem parenchyma [20,21]. Ray cells extend radially throughout the xylem and connect to the phloem, allowing for both the **lateral storage and remobilization** of NSCs into and out of the stem [22], which in turn supports the leakage and retrieval of solutes along the pathway [17].