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Anatomical insights into tree stem carbon storage: where do trees store starch and how to quantify it?

David Herrera-Ramirez (1), Henrik Hartman (1), Christine Römermann (2), Jan Muhr (1), Susan Trumbore (1), Fritz Schweingruber (3), and Carlos Sierra (1)

(1) Max Planck Institute for Biogeochemistry, Biogeochemical Processes, Hans Knöll str 10, Jena-Stadt, Germany , (2) Friedrich Schiller University Jena, Institute for Ecology and Evolution, Philosophenweg 16, 07743, Jena, Germany., (3) Swiss Federal Institute for Forest, Snow ad Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.

Trees store substantial amounts of non-structural carbon (NSC, primarily starch, soluble sugars and lipids) in parenchyma cells of woody tissues that can be subsequently used to survive stressful environmental conditions. Structural components of wood provide the infrastructure for storing and mobilizing starch reserves. Knowing how wood anatomy determines the starch dynamics is fundamental to understanding carbon allocation. In this contribution, we address the following questions: i) How can starch reserves in tree stem-wood tissues be reliably visualized and quantified? ii) Does the spatial distribution of starch reserves in the stem wood vary between different tree species that have different anatomical traits? And iii) do seasonal starch dynamics vary between tree species? We selected nine tropical tree species differing in the amount of parenchyma and in leaf phenology, occurring in the seasonally dry forest between the Amazon Forest and the Cerrado, Brasil. For each tree, we took two adjacent stem-wood cores and one from the opposite side, once in every season (dry and wet). The adjacent cores were used to validate, with a standard extraction method, a histological (micro-anatomical) method for measuring the spatial distribution and abundance of starch. We visualized and quantified with the histological method the starch distribution and spatial variability from the two opposing cores. After having stained the samples with Lugol's solution we measured the percentage of the area covered by starch granules on one-square-millimeter samples of the transversal slides from digital photos. These data were validated with concentrations obtained by hydrolysis (with α-amylase and amyloglucosidase) and extraction of starch from 2cm long segments from the adjacent core. The percentage of the area covered by starch in the transversal section was remarkably well-correlated with the percentage of starch extracted per volume of wood. Starch distributions varied substantially across the transversal section in each tree, but followed similar patterns within trees of the same species. For seven of the nine species, starch was stored mainly in parenchyma tissues, of both rays and axial parenchyma. For the two other species, most of the starch was stored in living xylem fibers. Some species showed clumping of starch in ray parenchyma while in others starch was randomly distributed in ray/axial parenchyma and living fibers. Also, for most of the species starch was stored in the most recent four centimeters of wood, but was practically absent in deeper wood layers. We expect to find quicker mobilization and potentially higher trade volume of starch in the seasonal dynamics of species with more parenchyma and bigger rays, whereas a more conservative behavior in the species with low amount of parenchyma. Our method proposed here thus underscores the influence of wood anatomical traits on starch distribution in tree stems. Our method allows quantifying starch stocks in stem wood and visualizing changes in the spatial distribution during the growth season. This information is necessary to understand what are the determinants that drive the allocation of carbon to tree storage and what does that imply for tree resilience to stressful environmental conditions.