



HAL
open science

Non-structural carbohydrates and morphological traits of leaves, stems and roots from tree species in different climates

Guangqi Zhang, Pascale Maillard, Zhun Mao, Loïc Brancheriau, Julien Engel, Bastien Gérard, Claire Fortunel, Jean Luc Maeght, Jordi Martínez-vilalta, Merlin Ramel, et al.

► **To cite this version:**

Guangqi Zhang, Pascale Maillard, Zhun Mao, Loïc Brancheriau, Julien Engel, et al.. Non-structural carbohydrates and morphological traits of leaves, stems and roots from tree species in different climates. BMC Research Notes, 2022, 15, 10.1186/s13104-022-06136-7 . hal-03736228

HAL Id: hal-03736228

<https://hal.inrae.fr/hal-03736228v1>

Submitted on 22 Jul 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.




Distributed under a Creative Commons Attribution 4.0 International License

DATA NOTE

Open Access



Non-structural carbohydrates and morphological traits of leaves, stems and roots from tree species in different climates

Guangqi Zhang^{1*} , Pascale Maillard², Zhun Mao¹, Loic Brancheriau³, Julien Engel¹, Bastien Gérard², Claire Fortunel¹, Jean-Luc Maeght¹, Jordi Martínez-Vilalta^{4,5}, Merlin Ramel¹, Sophie Nourissier-Mountou¹, Stéphane Fourtier¹ and Alexia Stokes¹

Abstract

Objectives: Carbon fixed during photosynthesis is exported from leaves towards sink organs as non-structural carbohydrates (NSC), that are a key energy source for metabolic processes in trees. In xylem, NSC are mostly stored as soluble sugars and starch in radial and axial parenchyma. The multi-functional nature of xylem means that cells possess several functions, including water transport, storage and mechanical support. Little is known about how NSC impacts xylem multi-functionality, nor how NSC vary among species and climates. We collected leaves, stem and root xylem from tree species growing in three climates and estimated NSC in each organ. We also measured xylem traits linked to hydraulic and mechanical functioning.

Data description: The paper describes functional traits in leaves, stems and roots, including NSC, carbon, nitrogen, specific leaf area, stem and root wood density and xylem traits. Data are provided for up to 90 angiosperm species from temperate, Mediterranean and tropical climates. These data are useful for understanding the trade-offs in resource allocation from a whole-plant perspective, and to better quantify xylem structure and function related to water transportation, mechanical support and storage. Data will also give researchers keys to understanding the ability of trees to adjust to a changing climate.

Keywords: Angiosperms, Non-structural carbohydrates, Fibers, Functional traits, Mediterranean, Parenchyma, Root, Temperate, Tropical, Vessels

Objective

Non-structural carbohydrates (NSC) are essential substrates for metabolic processes in trees, including respiration, osmoregulation, growth, reproduction and defense [1–4], as well as having major consequences for downstream processes such as microbial activity in the rhizosphere [5]. NSC is a product of photosynthesis and

comprises mainly soluble sugars involved in transport or immediate functions, and starch stored in different plant organs for future use and maintaining functionality when carbon demand is higher than supply (e.g., under severe drought stress) [6–9]. Therefore, understanding how patterns of NSC vary in trees will enable us to better evaluate the role of NSC in tree physiological processes and ecological strategies, especially across a broad range of species and climates [10].

The secondary xylem of angiosperms is generally composed of three specialized cell types including parenchyma, vessels and fibers (tracheids and fiber-tracheids may also be present), that perform storage, hydraulic and

*Correspondence: zh.guangqi@gmail.com

¹ AMAP, Université de Montpellier, CIRAD, CNRS, INRAE, IRD, 34000 Montpellier, France

Full list of author information is available at the end of the article



© The Author(s) 2022. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

Table 1 Overview of data files/data sets

Label	Name of data file/data set	File types (file extension)	Data repository and identifier (DOI or accession number)
Data file 1	Xylem_Stem_Root_Leaf_Trait data	MS Excel file (.xlsx)	Portail Data INRAE https://doi.org/10.15454/MU0HXX [23]

mechanical functions [11–13]. NSC are mainly stored in the live radial and axial parenchyma cells, therefore the size of the parenchyma fraction drives the capacity for NSC storage in trees [14–16]. In an attempt to disentangle how NSC and xylem traits are linked to tree physiological processes and ecological strategies, we collated data on stem and root NSC and xylem cell patterns, as well as leaf traits, from 90 tree species in temperate, Mediterranean and tropical climates. Our data will allow researchers to explore the direct relationships between leaf, stem and root NSC contents with patterns in xylem cell composition. To our knowledge, this dataset represents the largest freely available collection of data for NSC xylem and leaf traits measured simultaneously in adult trees from diverse climates. Detailed information on materials and methods can be found in the accompanying Excel file (Table 1).

Data description

Study sites and species

This study was conducted in a temperate forest (Luz-Saint-Sauveur, France), a Mediterranean forest (Montpellier, France) and a tropical forest (Paracou, French Guiana). A total 90 angiosperm species were collected which are commonly found in local forests, with 20 species in both temperate and Mediterranean climates and 50 species in the tropical climate (Table 1, file 1). For each species, we chose three, healthy, adult trees that usually had a stem diameter of between 0.05 and 0.4 m at a height of 1.3 m. We collected leaf and stem samples for all trees, as well as coarse root samples for 60 species ($n=20$ in each climate). Samples were collected at the end of August and early September 2019 for Mediterranean and tropical species and September 2020 for temperate species, when NSC storage should be close to its seasonal maximum [17–19]. We sampled all trees between 7am and midday, to reduce variability linked to photosynthate production. At a height of 1.3 m, three 0.05 m long cores were extracted from tree stems with a 4.3 mm diameter increment borer. To collect samples of roots, we excavated a single lateral root (0.02–0.05 m in diameter) and at a distance of 0.3–0.5 m from the base of the tree and extracted three increment cores or removed three 0.02 m long segments of root. We also collected one stem core from each tree in temperate and Mediterranean climates in March 2021 (before bud burst). In

total, 540 leaf samples, 930 stem cores and 540 root segments were collected.

Measurement of leaf and xylem functional traits

A total of 270 leaf samples, 390 stem samples and 180 root samples were used to determine NSC, carbon (C) and nitrogen (N) measurements. For NSC content, a colorimetric method [20] was performed on all leaf samples, and a subsample of stems ($n=113$) and roots ($n=140$). C and N content were measured in a sub-sample of leaves ($n=110$), stems ($n=113$) and all root samples, using an elemental analyzer (CHN model EA 1108, Milan, Italy). Then, near infra-red spectroscopy (NIRS) [21] was performed on all samples and calibration models developed using data obtained from the analytical methods to predict soluble sugars, starch, C and N in the three organs (Table 1, file 1).

Cross-sections of 15–20 μm thick for stem ($n=270$) and root ($n=180$) samples were cut with a sliding microtome and stained with a mixture of safranin and alcian blue. Microphotographs of transversal sections were taken where radial and axial parenchyma fractions, vessel fractions, mean vessel area, mean vessel diameter, vessel density, mean vessel hydraulic diameter and theoretical specific xylem hydraulic conductivity were determined [22] (Table 1, file 1).

Specific leaf area ($n=270$) was determined using leaf area and dry mass. Stem wood density ($n=270$) and root wood density ($n=180$) were defined as oven-dry mass divided by fresh volume which measured by water displacement method (Table 1, file 1).

Limitations

Root NSC data were only collected for 60 species ($n=20$ in each climate type). It was not possible to collect NSC in samples from tropical trees over two different seasons within a 12-month time period because of travel restrictions linked to the COVID pandemic. However, there is significantly less seasonal variability in NSC in tropical trees [10], compared to Mediterranean and temperate species, therefore we do not consider this limitation as detrimental to the quality of data.

Abbreviations

NSC: Non-structural carbohydrates; C: Carbon; N: Nitrogen; NIRS: Near infra-red spectroscopy.

Acknowledgements

We are grateful to N. Boutahar (CIRAD) and J. Cazal (INRAE) for their help with field and laboratory work. We thank G. Derroire and A. Dourdain for their aid with logistical arrangements and field authorizations in French Guyana. The collecting of genetic resources in French Guyana was authorized by the French Government (APA No. 1371201). We kindly thank to managers of state-owned land for their collaboration and to B. Dupin (Eco-Altitude) for permission to sample trees on private property at Luz-Saint-Sauveur, France. The authors would like to thank SILVATECH (<https://doi.org/10.15454/1.5572400113627854E12>) from UMR 1434 SILVA, 1136 IAM, 1138 BEF and 4370 EA LERMAB from the research center INRAE Grand-Est Nancy for its contribution to NSC analyses. The SILVATECH facility is supported by the French National Research Agency through the Laboratory of Excellence ARBRE (ANR-11-LABX-0002-01).

Author contributions

GZ and AS prepared the manuscript. GZ, AS, PM, ZM, JE, CF, JLM, JMV, MR, SNM, SF conducted fieldwork. GZ, AS, LB, BG performed laboratory analyses. GZ, ZM, AS analyzed data. All authors read and approved the final manuscript.

Funding

This study was supported by China Scholarship Council (PhD bursary for GZ) and a Grant from Investissement d'Avenir Grants of the ANR, France (CEBA: ANR-10-LABX-25-01).

Availability of data and materials

The data and methods described in this Data note can be freely and openly accessed on Portail Data INRAE under <https://doi.org/10.15454/MU0HXX>. Please see Table 1 and reference [23] for details and links to the data.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹AMAP, Université de Montpellier, CIRAD, CNRS, INRAE, IRD, 34000 Montpellier, France. ²SILVA, INRAE, Université de Lorraine, Agroparistech, Centre de Recherche Grand-Est Nancy, 54280 Champenoux, France. ³CIRAD, Université de Montpellier, UR BioWooEB, 34000 Montpellier, France. ⁴CREAF, Bellaterra, 08193 Cerdanyola del Vallès, Catalonia, Spain. ⁵Universitat Autònoma Barcelona, Bellaterra, 08193 Cerdanyola del Vallès, Catalonia, Spain.

Received: 2 March 2022 Accepted: 23 June 2022

Published online: 15 July 2022

References

- Kozłowski T. Carbohydrate sources and sinks in woody plants. *Bot Rev.* 1992;58:107–222.
- Morin X, Ameglio T, Ahas R, Kurz-Besson C, Lanta V, Lebourgeois F, et al. Variation in cold hardiness and carbohydrate concentration from dormancy induction to bud burst among provenances of three European oak species. *Tree Physiol.* 2007;27:817–25.
- Sala A, Woodruff DR, Meinzer FC. Carbon dynamics in trees: feast or famine? *Tree Physiol.* 2012;32:764–75.
- Morris H, Hietala AM, Jansen S, Ribera J, Rosner S, Salmeia KA, Schwarze FW. Using the CODIT model to explain secondary metabolites of xylem in defence systems of temperate trees against decay fungi. *Ann Bot.* 2020;125:701–20.
- Schiestl-Aalto P, Ryhti K, Mäkelä A, Peltoniemi M, Bäck J, Kulmala L. Analysis of the NSC storage dynamics in tree organs reveals the allocation to

- belowground symbionts in the framework of whole tree carbon balance. *Front For Glob Change.* 2019;2:17.
- Anderegg WRL, Anderegg LDL. Hydraulic and carbohydrate changes in experimental drought-induced mortality of saplings in two conifer species. *Tree Physiol.* 2013;33:252–60.
- Wiley E, Huepenbecker S, Casper BB, Helliker BR. The effects of defoliation on carbon allocation: can carbon limitation reduce growth in favour of storage? *Tree Physiol.* 2013;33:1216–28.
- Klein T, Hoch G. Tree carbon allocation dynamics determined using a carbon mass balance approach. *New Phytol.* 2015;205:147–59.
- Furze ME, Huggett BA, Aubrecht DM, Stolz CD, Carbone MS, Richardson AD. Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. *New Phytol.* 2019;221:1466–77.
- Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, et al. Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecol Monogr.* 2016;86:495–516.
- Pratt RB, Jacobsen AL. Conflicting demands on angiosperm xylem: tradeoffs among storage, transport and biomechanics. *Plant Cell Environ.* 2017;40:897–913.
- Chen Z, Zhu S, Zhang Y, Luan J, Li S, Sun P, et al. Tradeoff between storage capacity and embolism resistance in the xylem of temperate broadleaf tree species. *Tree Physiol.* 2020;40:1029–42.
- Plavcová L, Gallenmüller F, Morris H, Khatamirad M, Jansen S, Speck T. Mechanical properties and structure–function trade-offs in secondary xylem of young roots and stems. *J Exp Bot.* 2019;70:3679–91.
- Plavcová L, Hoch G, Morris H, Ghiasi S, Jansen S. The amount of parenchyma and living fibers affects storage of nonstructural carbohydrates in young stems and roots of temperate trees. *Am J Bot.* 2016;103:603–12.
- Zhang G, Mao Z, Fortunel C, Martínez-Vilalta J, Viennois G, Maillard P, et al. Parenchyma fractions drive the storage capacity of non-structural carbohydrates across a broad range of tree species. *Am J Bot.* 2022;109:535–49.
- Rodríguez-Calcerrada J, López R, Salomón R, Gordaliza GG, Valbuena-Carabaña M, Oleksyn J, Gil L. Stem CO₂ efflux in six co-occurring tree species: underlying factors and ecological implications. *Plant Cell Environ.* 2015;38:1104–15.
- Palacio S, Camarero JJ, Maestro M, Alla AQ, Lahoz E, Montserrat-Martí G. Are storage and tree growth related? Seasonal nutrient and carbohydrate dynamics in evergreen and deciduous Mediterranean oaks. *Trees.* 2018;32:777–90.
- Würth MK, Pelaez-Riedl S, Wright SJ, Körner C. Non-structural carbohydrate pools in a tropical forest. *Oecologia.* 2005;143:11–24.
- Richardson AD, Carbone MS, Keenan TF, Czimczik CI, Hollinger DY, Murakami P, et al. Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. *New Phytol.* 2013;197:850–61.
- Black M, Corbineau F, Grzesik M, Guy P, Come D. Carbohydrate metabolism in the developing and maturing wheat embryo in relation to its desiccation tolerance. *J Exp Bot.* 1996;47:161–9.
- Ramirez JA, Posada JM, Handa IT, Hoch G, Vohland M, Messier C, Reu B. Near-infrared spectroscopy (NIRS) predicts non-structural carbohydrate concentrations in different tissue types of a broad range of tree species. *Methods Ecol Evol.* 2015;6:1018–25.
- Scholz A, Klepsch M, Karimi Z, Jansen S. How to quantify conduits in wood? *Front Plant Sci.* 2013. <https://doi.org/10.3389/fpls.2013.00056>.
- Zhang G, Stokes A. Xylem_Stem_Root_Leaf_Trait data. Portail Data INRAE. 2022. <https://doi.org/10.15454/MU0HXX>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.