

The isotopic composition of phloem water and its relations to xylem water at daily and sub-daily resolutions

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Background

Research Questions

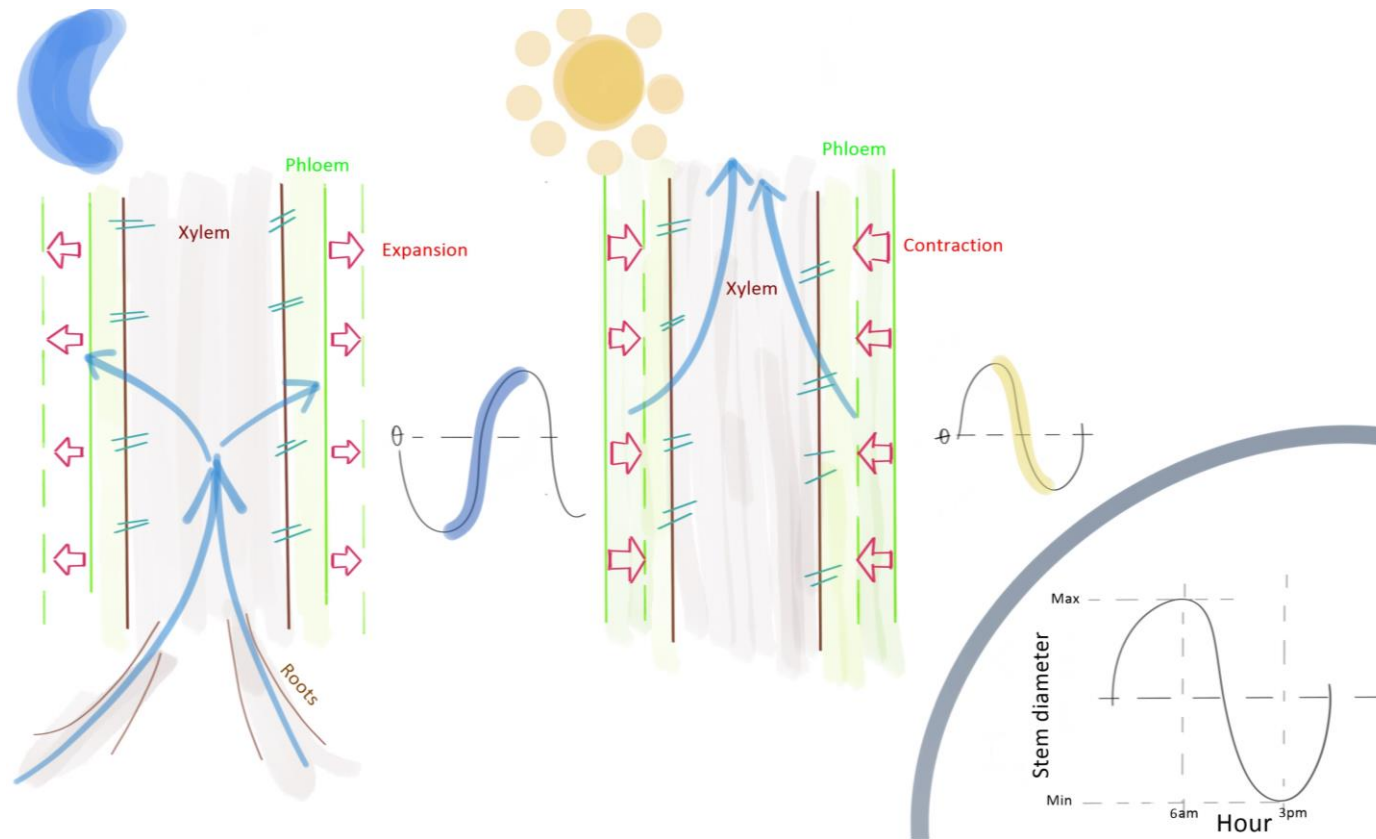
Experimental Design

Results

Discussion & Summary

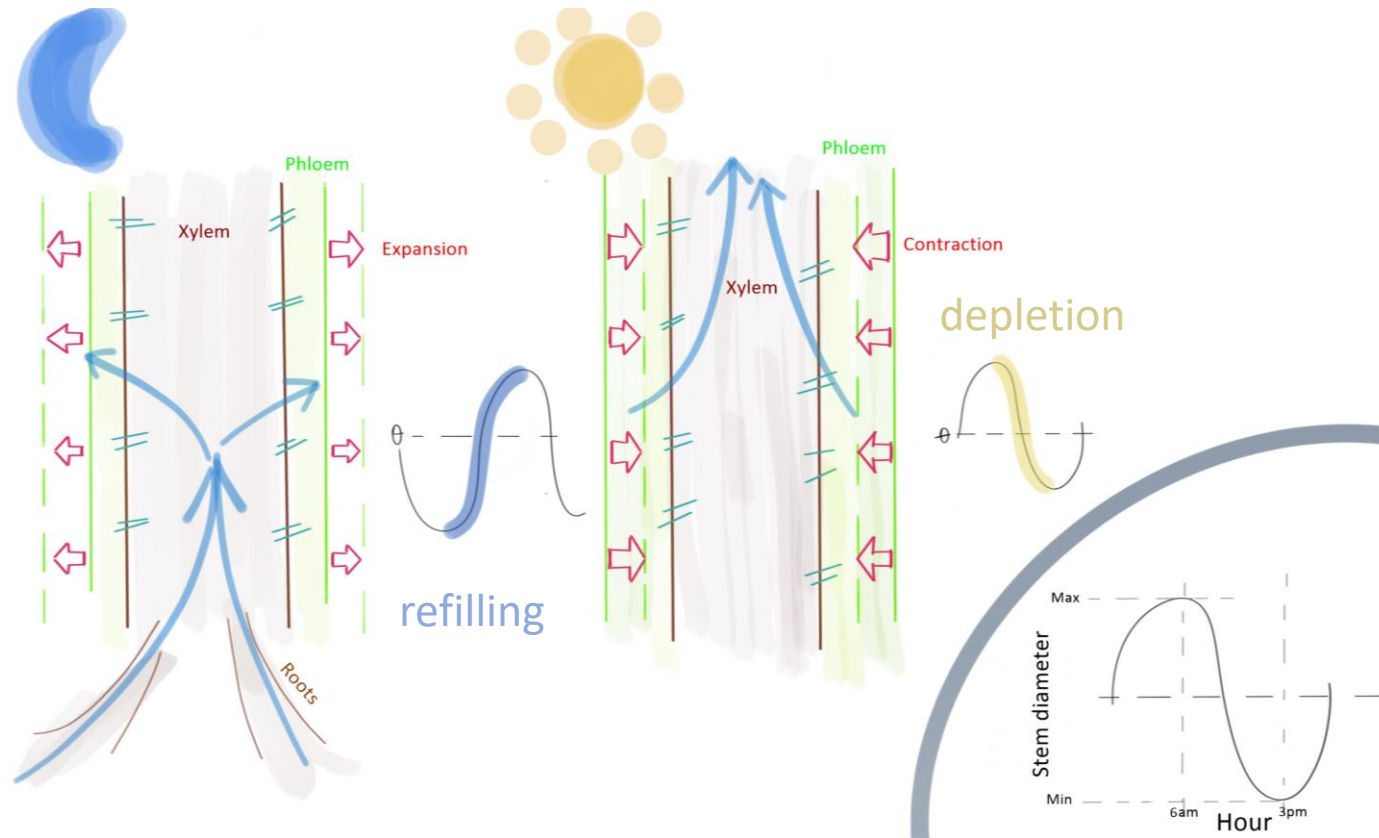
Contact

Tree water transport is not *unidirectional* (i.e. from roots to leaves)



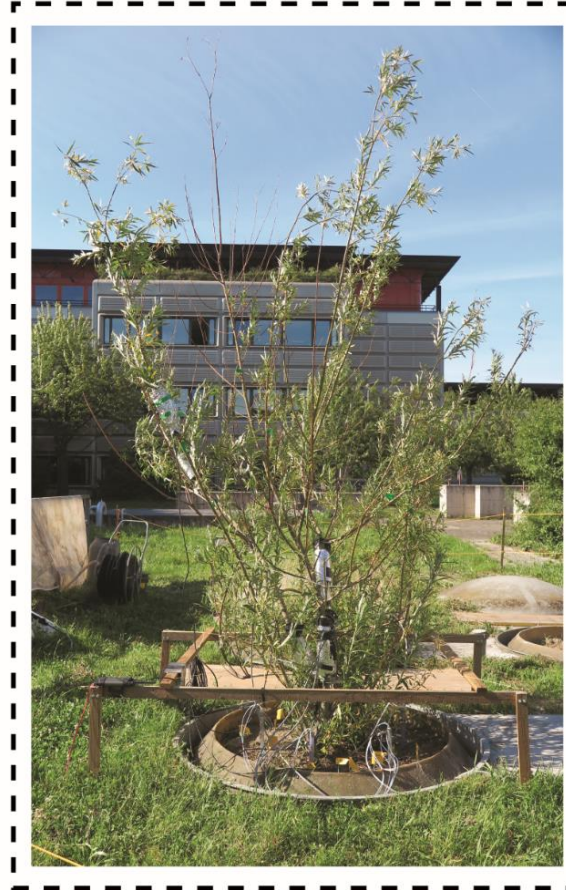
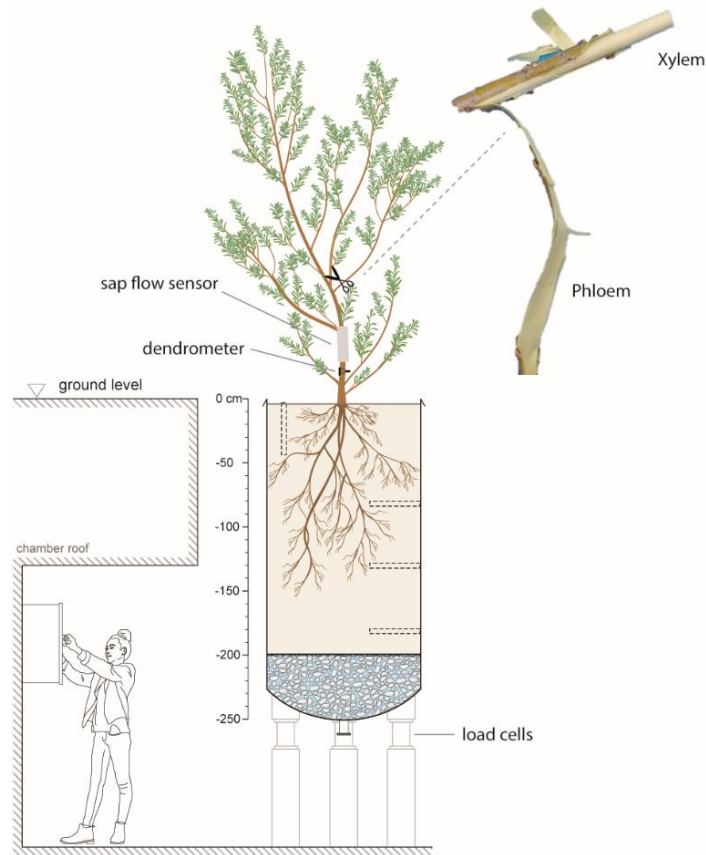
- Water transported and stored in the phloem can actively participate in the transpiration stream
- Tree hydraulic models and field experiments (e.g. Steppe et al., 2006; Hölttä et al., 2009; De Schepper & Steppe, 2010; Pfautsch et al., 2015; Hubeau & Steppe, 2015) have now shown the tight hydraulic linkage between xylem and phloem
- This important storage of phloem water has yet to be considered in dual-isotope investigation of tree water source

Daily and Sub-daily resolution phloem and xylem water



- 1) How do isotope ratios in phloem and xylem covary?
- 2) How does it change during stem diurnal cycle (*i.e.* during depletion and refilling of phloem water)?

Experimental setup: Lysimeter & *Salix viminalis*



- We conducted our controlled experiment in a large lysimeter situated in an open field planted with *Salix viminalis*
- We monitored tree hydrodynamics using a point dendrometers (Ecomatik; type DD-S) and heat balance sensors (EXO-Skin SGA19; SGA 25, SGA 25 Dynamax) to monitor stem diameter variation and sap flow, respectively.
- We sampled the isotopic composition of xylem and phloem water simultaneously from June 4 to June 29, 2018. We collected xylem and phloem samples from the same branch.

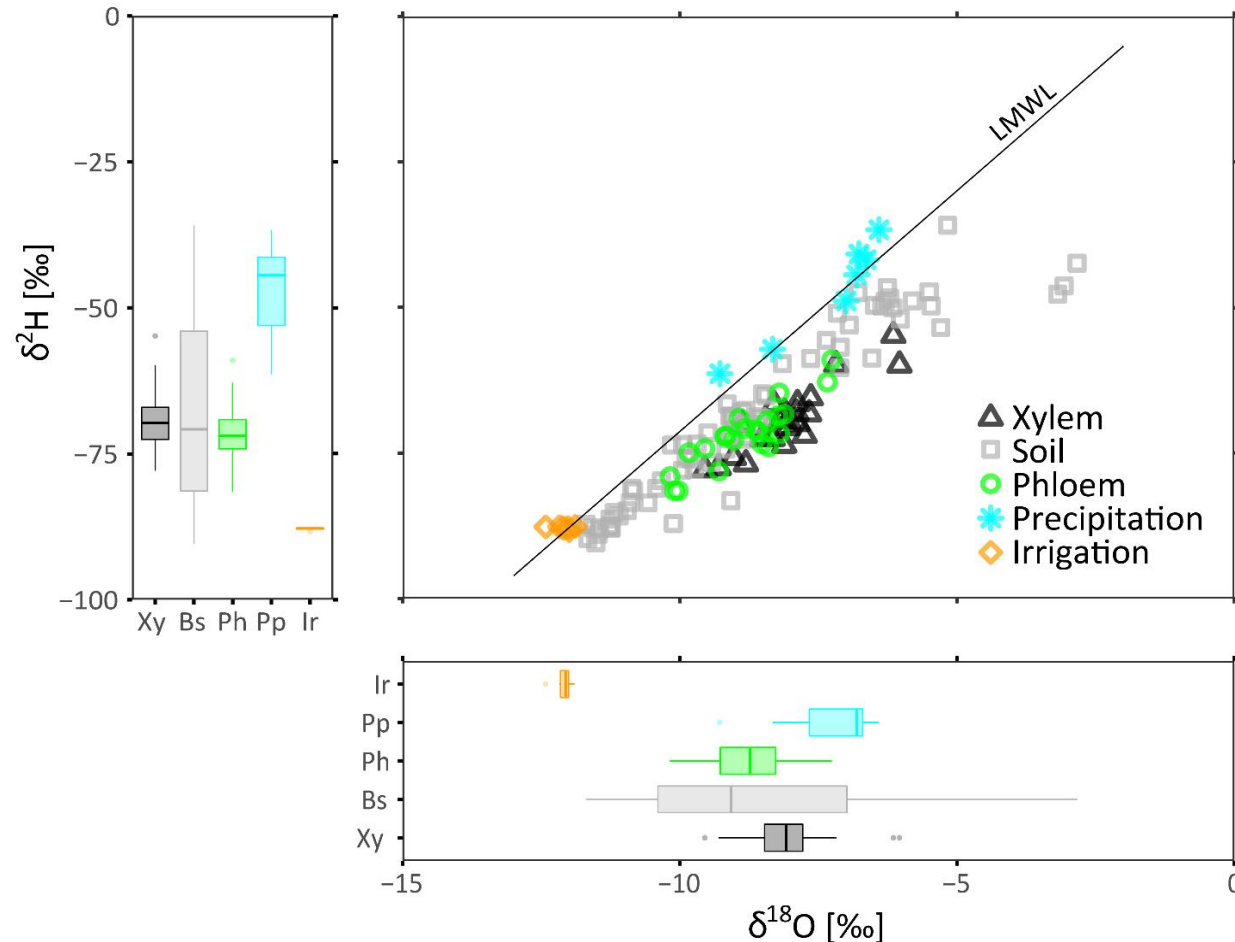
Phloem and xylem water extraction and isotopic analysis



- We extracted xylem and phloem water using a cryogenic vacuum distillation system following Koeniger *et al.*, (2011)
- We analysed the isotopic composition of xylem and phloem using isotope ratio mass spectrometry (IRMS). $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values are expressed in delta notation relative to the international standard V-SMOW
- We computed the isotopic $\delta^2\text{H}$ and $\delta^{18}\text{O}$ difference between phloem and xylem pools (expressed at per mil, ‰) as:

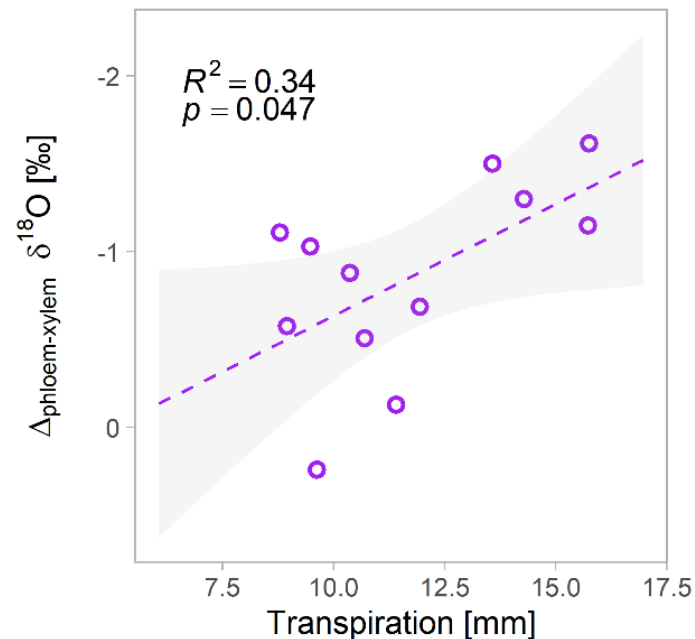
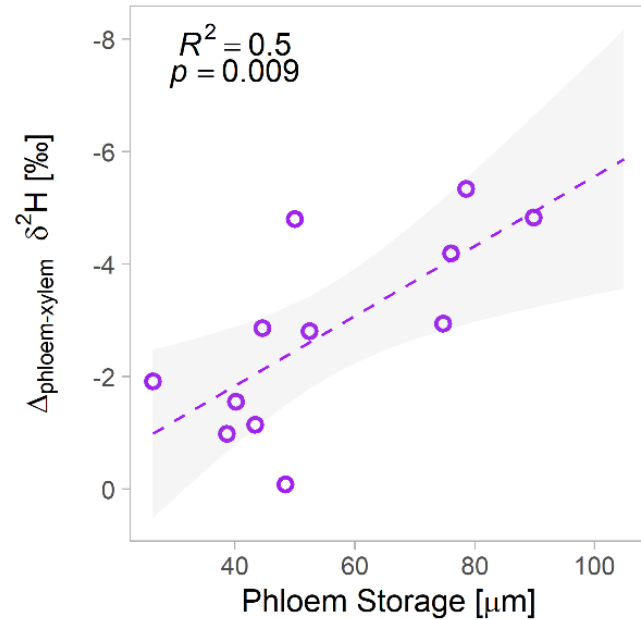
$$\Delta_{\text{phloem-xylem}} = \delta_{\text{phloem}} - \delta_{\text{xylem}}$$

Xylem water is more enriched in heavy isotopes than phloem water



- Phloem and xylem isotopic composition ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) was significantly distinct throughout the sampling period (Wilcoxon signed-rank test, $p < 0.001$).
- Our data shows that xylem water plotted further away from the local meteoric water line (LMWL) than phloem water and was systematically more enriched in ^{18}O and ^2H than phloem water (on average + 0.66 ‰ $\delta^{18}\text{O}$ and + 2.05 ‰ $\delta^2\text{H}$).
- Despite been statistically distinct, xylem and phloem water isotopic composition was significantly correlated in both $\delta^{18}\text{O}$ ($r = 0.75$) and $\delta^2\text{H}$ ($r = 0.89$) throughout the experiment.

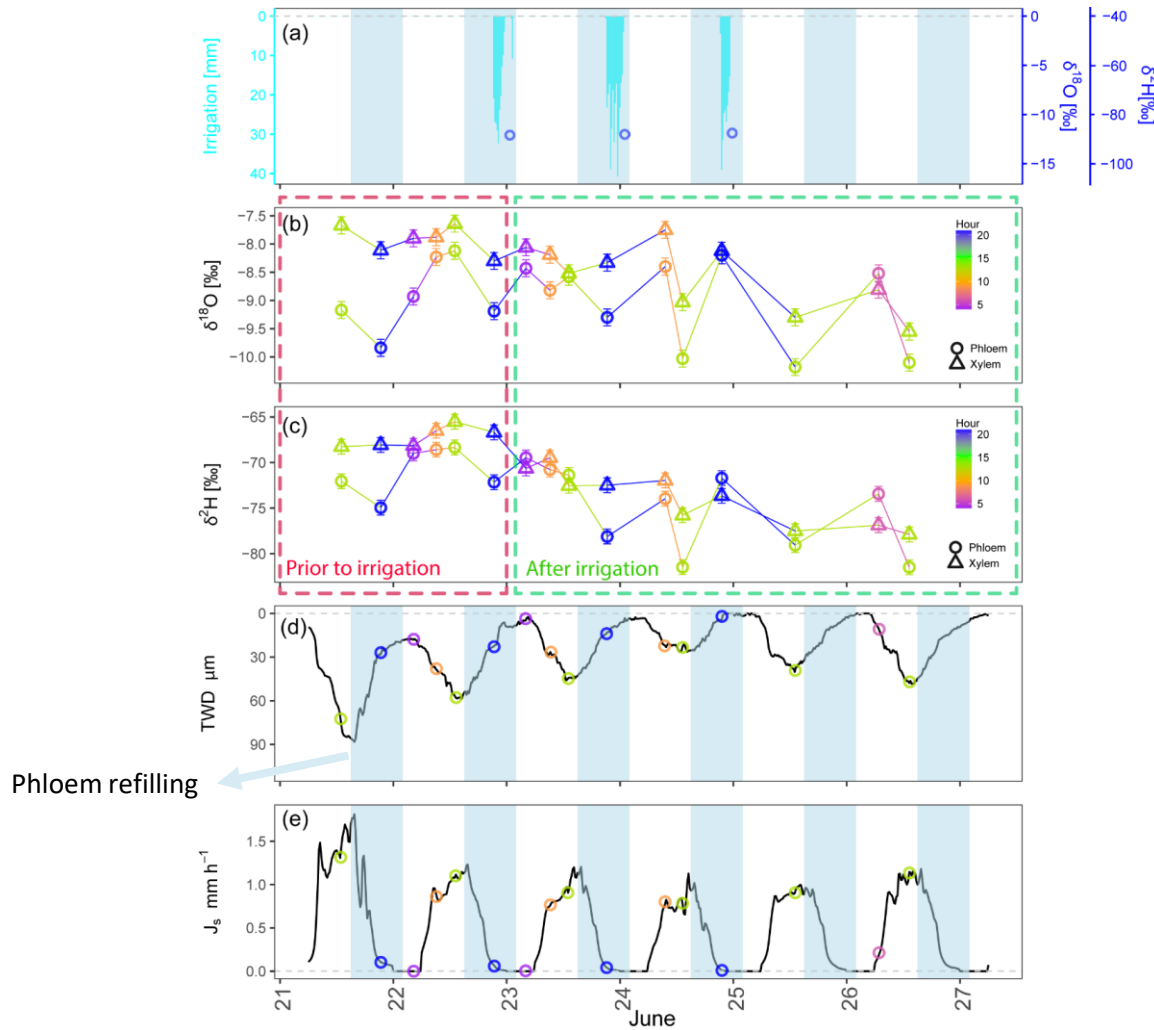
Integrated daily phloem water use and Δ phloem-xylem



- The $\delta^2\text{H}$ difference (Δ phloem-xylem) between phloem and xylem was statistically shown to increase with the increase in daily use of phloem water, while $\delta^{18}\text{O}$ difference between phloem and xylem increases with the increase in transpiration rate.

Sub-daily resolution: Phloem and xylem water and tree hydrodynamics

- We observed variability in the xylem and phloem isotopic composition throughout the diurnal cycle (*e.g.* nighttime, predawn, morning and midday)
- The largest difference between phloem and xylem is observed during phloem refilling (blue circles; shaded blue), while the smallest difference is observed at predawn (purple circles).
- Xylem and phloem were distinct in both, $\delta^{18}\text{O}$ ($p < 0.01$) and $\delta^2\text{H}$ ($p < 0.05$) prior to irrigation. Despite some small differences in isotopic composition during irrigation, they were not significantly distinct in both $\delta^{18}\text{O}$ and $\delta^2\text{H}$.



Phloem water is rarely reported, and only one isotope ($\delta^{18}\text{O}$ or $\delta^2\text{H}$) is reported per study

HYDROGEN ISOTOPIC FRACTIONATION OF WATER PASSING THROUGH TREES

by

R. L. WERSHAW, IRVING FRIEDMAN and S. J. HELLER

U.S. Geological Survey

and

P. A. FRANK

Agricultural Research Service

1966

Utilization of oxygen-18 and deuterium in stem flow for the identification of transpiration sources: soil water versus groundwater in sand dune terrain

E. M. ADAR & I. GEV

*The Jacob Blaustein Institute for Desert Research, and Department of Geology,
Ben Gurion University of the Negev, Sede Boker Campus, Sede Boker 84990,
Israel*

1995

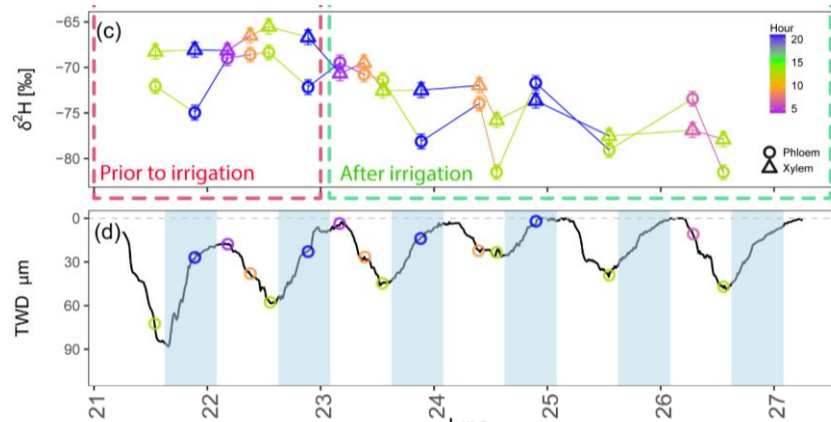
Environmental and physiological controls over oxygen and carbon isotope composition of Tasmanian blue gum, *Eucalyptus globulus*

LUCAS A. CERNUSAK,¹⁻³ GRAHAM D. FARQUHAR¹ and JOHN S. PATE⁴

2005

- Our results showed that on average *S. viminalis* xylem water was more enriched in heavy isotopes than phloem water.
- Our work supports the early findings from Wershaw et al (1966) that showed phloem water was more depleted in ^2H than xylem water. But, we observed larger offsets.
- Adar et al., (1995) and Cernusak et al. (2005) showed that phloem water was more enriched in ^{18}O than xylem water.
- Similarly to our observations, Cernusak et al., (2005) also noted temporal variability in the difference between phloem and xylem water isotopic composition.

What mechanisms could explain phloem water depleted isotopic values?



Effects of the hydraulic coupling between xylem and phloem on diurnal phloem diameter variation

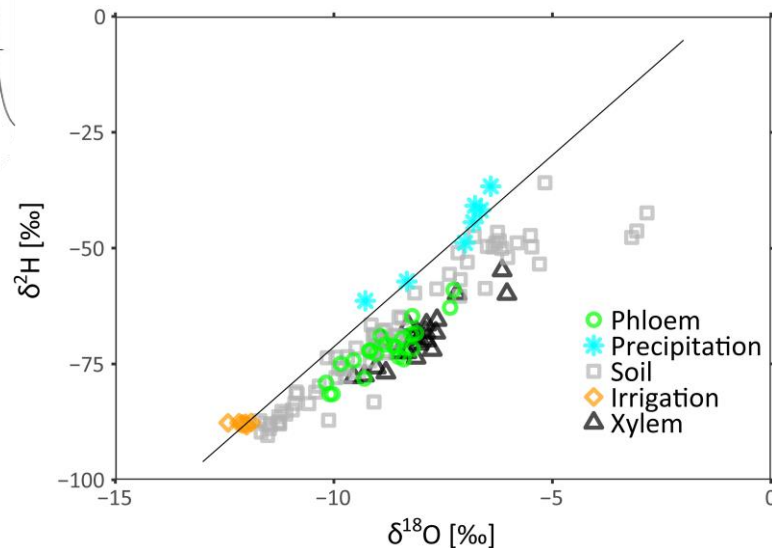
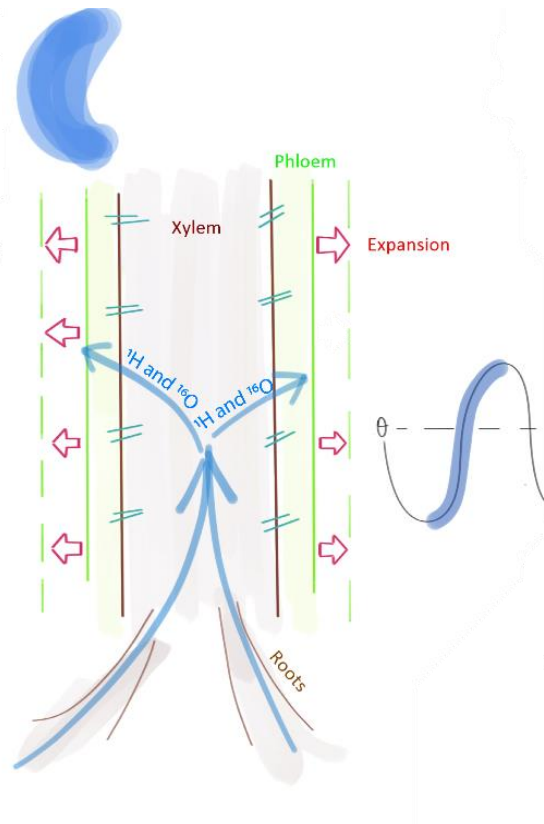
SANNA SEVANTO^{1,2*}, TEEMU HÖLTÄ³ & N. MICHELE HOLBROOK¹

Could rapid diameter changes be facilitated by a variable hydraulic conductance?

KATHY STEPPE^{1,2}, HERVÉ COCHARD^{2,3}, ANDRÉ LACOINTE^{2,3} & THIERRY AMÉGLIO^{2,3}

- The cell-to-cell pathway modulated by aquaporins have been suggested as the main pathway for water movement between xylem and phloem (Sevanto et al. 2011)
- Steppe et al. (2012) suggested that xylem-phloem radial flow is modulated by aquaporins when demands are high, while, apoplastic transport takes place when hydraulic demands are low.
- Additionally, aquaporins have shown lower osmotic permeability of $^2\text{H}_2^{16}\text{O}$ compared to $^1\text{H}_2^{16}\text{O}$ (Mamonov et al., 2007)

What mechanisms could explain phloem water depleted isotopic values?



- We hypothesize that when water enters the xylem in the roots and moves into the phloem via aquaporins, phloem is preferentially refilled with lighter isotopes (^1H and ^{16}O).
- Xylem water may also become slightly enriched in heavy isotopes (^2H and ^{18}O) with the preferential transport of lighter isotopes into the phloem.
- Would phloem water explain small fractionation observed in xylem water?
- We advocate for more studies sampling phloem water along with xylem across different species and wetness conditions.

Would you like to further discuss these findings? Or have questions?

Email me or find me on Twitter and Research Gate



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Magali F. Nehemy



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References in this presentation

- Adar EM, Gev I, Lipp J, Yakir D, Gat J, Cohen Y (The JBI for DR. 1995.** Utilization of oxygen-18 and deuterium in stem flow for the identification of transpiration sources: soil water versus groundwater in sand dune terrain. *Application of tracers in arid zone hydrology (United Kingdom)*.
- Cernusak LA, Farquhar GD, Pate JS. 2005.** Environmental and physiological controls over oxygen and carbon isotope composition of Tasmanian blue gum, *Eucalyptus globulus*. *Tree Physiology* **25**: 129–146.
- De Schepper V, Steppe K. 2010.** Development and verification of a water and sugar transport model using measured stem diameter variations. *Journal of Experimental Botany* **61**: 2083–2099.
- Hölttä T, Mencuccini M, Nikinmaa E. 2009.** Linking phloem function to structure: Analysis with a coupled xylem–phloem transport model. *Journal of Theoretical Biology* **259**: 325–337.
- Hubeau M, Steppe K. 2015.** Plant-PET Scans: In Vivo Mapping of Xylem and Phloem Functioning. *Trends in Plant Science* **20**: 676–685.
- Mamonov AB, Coalson RD, Zeidel ML, Mathai JC. 2007.** Water and deuterium oxide permeability through aquaporin 1: MD predictions and experimental verification. *The Journal of General Physiology* **130**: 111–116.
- Pfautsch S, Renard J, Tjoelker MG, Salih A. 2015b.** Phloem as Capacitor: Radial Transfer of Water into Xylem of Tree Stems Occurs via Symplastic Transport in Ray Parenchyma. *Plant Physiology* **167**: 963–971.
- Sevanto S, Hölttä T, Holbrook NM. 2011.** Effects of the hydraulic coupling between xylem and phloem on diurnal phloem diameter variation. *Plant, Cell & Environment* **34**: 690–703.
- Steppe K, Cochard H, Lacointe A, Améglio T. 2012.** Could rapid diameter changes be facilitated by a variable hydraulic conductance? *Plant, Cell & Environment* **35**: 150–157.
- Steppe K, De Pauw DJW, Lemeur R, Vanrolleghem P a. 2006.** A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. *Tree physiology* **26**: 257–273.