

5. Xylem	W ü r z b u r g
International Meeting	19 - 21 September
XIM5	2 0 2 2

— **Book of Abstracts** —

5th Xylem International Meeting

Book of Abstracts

The **5th Xylem International Meeting** is held from September 19 to September 21, 2022 at the University of Würzburg. It is hosted by the Department of Botany II (Ecophysiology and Vegetation Ecology) of the Julius-von-Sachs Institute for Biosciences of the University of Würzburg.

Local organizing committee

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XIM scientific committee

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Program

Program overview

	19 Sep 2022	20 Sep 2022	21 Sep 2022	22 Sep 2022
Time	Monday	Tuesday	Wednesday	Thursday
09-10		Topic sessions	Topic sessions	Excursions
10-11	Registration			
11-12				
12-13	Topic sessions			
13-14				
14-15				
15-16				
16-17			Closing ceremony	
17-18				
18-19				
19-20	Ice breaker		Conference dinner	
20-21				
21-22				

Monday, September 19

10:00 - 12:00 **Registration**

12:00 - 12:30 **Welcome and opening ceremony**

Session 1: Evolutionary history (Chair: Delzon, Sylvain)

12:30 - 13:00	1.0	Pittermann, Jarmila	Keynote: Xylem attributes shaped the evolution of Eupolypod ferns
13:00 - 13:15	1.1	Morris, Hugh	Co-evolution of axial parenchyma and vessels in relation to water transport in woody angiosperms reveals coordinated functional adaptation to climate across biomes
13:15 - 13:30	1.2	Corso, Deborah	Evolution of xylem vulnerability to cavitation in cereal crops: the downside of domestication and selection in wheat (<i>Triticum</i> sp.)
13:30 - 13:45	1.3	Lens, Frederic	Drought triggered woodiness on islands worldwide
13:45 - 14:00	1.4	Bouda, Martin	Drought resistance as a primary driver of stelar evolution in early vascular plants
14:00 - 14:15	1.5	Guzmán-Delgado, Paula	Rehydration dynamics via aerial surfaces – a mechanistic and evolutionary approach

14:15 - 15:15 Coffee break and poster session (posters of Session 7 & 8)

Session 2: Variability in plant hydraulic traits (Chair: Werner, Christiane)

15:15 - 15:45	2.0	Ramírez-Valiente, José	Keynote: Phenotypic plasticity of hydraulic traits in a global change context
15:45 - 16:00	2.1	Hammond, William	The global vulnerability of plant xylem
16:00 - 16:15	2.2	Gauthey, Alice	Long-term acclimation to soil moisture regulates thresholds of photosynthesis and thermoregulation capacity of <i>Pinus sylvestris</i>
16:15 - 16:30	2.3	Smith-Martin, Chis	Inter- and intra-specific variation among tree populations in their vulnerability to drought across a rainfall gradient in Puerto Rico

16:30 - 17:00 Coffee break

17:00 - 17:15	2.4	Andriantelomanana, Tsiky	Understanding the effects of acclimation to water deficit on the internal water storage dynamics of <i>Populus tremula</i> x <i>alba</i> during extreme drought
17:15 - 17:30	2.5	Feng, Feng	To everything there is a season, including xylem vulnerability
17:30 - 17:45	2.6	Hesse, Benjamin	Degree of isohydry in mature European beech and Norway spruce and strategy adjustments under repeated summer drought
17:45 - 18:00	2.7	Haberstroh, Simon	Hydraulic strategies of two woody Mediterranean species are dynamic

19:00 - 22:00 **Icebreaker** (Staatlicher Hofkeller Würzburg)

Tuesday, September 20

Session 3: Plant hydraulic models (Chair: Marlin-StPaul, Nicolas)

09:00 - 09:30	3.0	Cochard, Hervé	Keynote: Trait-based modeling of plant hydraulics
09:30 - 09:45	3.1	Ruffault, Julien	Assessing the vulnerability of forest ecosystems to drought and fire with the plant-hydraulics model SurEau-Ecos
09:45 - 10:00	3.2	Ziegler, Camille	Interspecific variability in physiological thresholds during dehydration reveals contrasting drought-response strategies and vulnerability to hydraulic failure in rainforest tree saplings
10:00 - 10:15	3.3	Waite, Pierre-André	Time to die: multilevel coordinated response and desiccation time during drought of 12 temperate tree species
10:15 - 10:30	3.4	Bozonnet, Cyril	Modelling the cycles of winter stem pressure in walnut tree
10:30 - 10:45	3.5	Hildebrandt, Anke	Evaluating the plant and soil limitation to root water uptake using thermodynamics
10:45 - 11:15			Coffee break

Session 4: Peripheral hydraulics (Chair: Ahmed, Mutez)

11:15 - 11:45	4.0	Hedrich, Rainer	Keynote: New insight in to guard cell networks controlling stomatal action
11:45 - 12:00	4.1	Brodribb, Timothy	Does xylem cavitation lead to foliar catastrophe?
12:00 - 12:15	4.2	Creek, Danielle	Leaky leaves: the importance of gmin in determining time to death in wheat under drought
12:15 - 12:30	4.3	Trueba, Santiago	Leaf dehydration dynamics after stomatal closure: from non-vascular plants to angiosperms
12:30 - 14:00			Lunch break
14:00 - 14:15	4.4	McAdam, Scott	The importance of stomatal closure in preventing embolism
14:15 - 14:30	4.5	Tonet, Vanessa	The point of non-recovery of leaf photosynthetic activity and gas exchanges is determined by the spread of cavitation in leaf minor veins
14:30 - 14:45	4.6	Lintunen, Anna	Tree water loss through bark in dry conditions
14:45 - 15:00	4.7	Mas, Eugénie	Soil drought has a more decisive impact than temperature on leaf hydraulic traits during hot droughts in temperate trees
15:00 - 15:15	4.8	Rodriguez-Dominguez, Celia	Root shrinkage and recovery during edaphic drought: insights from high-resolution synchrotron X-ray CT images
15:15 - 15:30	4.9	Bortolami, Giovanni	The potential role of root pressure on resistance to drought in tomato
15:30 - 16:30			Coffee break and poster session (posters of Session 3, 4 & 6)

Session 5: Concepts and methods (Chair: Mayr, Stefan)

16:30 - 17:00	5.0	Jansen, Steven	Keynote: The functional significance of porous media and polar lipids for fluid transport in angiosperm xylem
17:00 - 17:15	5.1	Domec, Jean-Cristophe	Catastrophic Hydraulic Failure and Tipping Points in Plants
17:15 - 17:30	5.2	Pereira, Luciano	Dissolved gas in xylem sap is affected by water potential and temperature, but does not follow Henry's law for bulk solutions
17:30 - 17:45	5.3	Peters, Richard	Define the water-use strategy: A case-study on hydraulic mechanisms regulating water use of European tree species during drought
17:45 - 18:00	5.4	Krieger, Louis	Xylem hydraulic conductivity measurements during flow-controlled experiments suggest the presence of gas bubbles that move with the flow and accumulate at vessel ends

Wednesday, September 21

Session 6: Drought- and heat-induced tree mortality (Chair: Rühr, Nadine)

09:00 - 09:30	6.0	Grossiord, Charlotte	Keynote: Disentangling the impacts of atmospheric and soil droughts on forests
09:30 - 09:45	6.2	Wagner, Yael	If a cavitation event occurred in the forest and no one was around to measure it: the role of embolism in the survival and recovery of Aleppo pine from drought
09:45 - 10:00	6.3	Mantova, Marylou	Dying of thirst: when hydraulic failure leads to cell death
10:00 - 10:15	6.4	Gori, Antonella	Mechanisms underlying holm oak recovery after water stress: is the carbon reserves consumption unavoidable to maintain xylem hydraulic functionality?
10:15 - 10:45		Coffee break	
10:45 - 11:00	6.5	Link, Roman	Mutually inclusive mechanisms of drought--induced tree mortality
11:00 - 11:15	6.6	Skelton, Robert	Hydraulic safety margins in South African plant communities: how close are they to the edge?
11:15 - 11:30	6.7	Moreno, Myriam	Mixing isohydric and anisohydric tree species increases water use but improves hydraulic safety margins during extreme drought
11:30 - 11:45	6.8	Bär, Andreas	When the heat was on: long-term limitations of xylem hydraulics after forest fires
11:45 - 13:00		Lunch break	

Session 7: Xylem structure and function (Chair: Cardoso, Amanda)

13:00 - 13:30	7.0	McElrone, Andrew	Keynote: Save it for a rainy day? Evaluating dynamic changes in conduit functional status relative to water storage of neighboring cells across several woody plant species
13:30 - 13:45	7.1	Chhajed, Shubham	Hydraulic strategies associated with water storage in woody plants across water availability gradient
13:45 - 14:00	7.2	Hietz, Peter	Distinguishing genetic, ontogenetic and spurious xylem adaptations to aridity
14:00 - 14:15	7.3	Larter, Maximilian	Xylem functional trait trade-offs and tree species responses to drought and cold stresses in NA and EU forests
14:15 - 14:30	7.4	Anfodillo, Tommaso	Maintaining leaf hydraulic conductance constant for constant carbon cost: the interplay of xylem traits
14:30 - 14:45	7.5	Petit, Gai	Two path length effects emerging from ontogenetically stable axial xylem design affect the conductance of inner sapwood rings
14:45 - 15:45		Coffee break and poster session	(posters of Session 1, 2 & 5)

Session 8: Ecosystem water fluxes (Chair: Torres-Ruiz, José)

15:45 - 16:00	8.1	Werner, Christiane	$2H_2O$ Pulse-Labeling traces the role of different hydraulic strategies, utilization of deep water reserves and water transport times on ecosystem drought response and recovery
16:00 - 16:15	8.2	Tomasella, Martina	Bedrock as a water source for trees under drought: experimental evidence and model simulations
16:15 - 16:30	8.3	Poyatos, Rafael	Tree water use resilience from sap flow data: towards a characterisation of tree drought responses in their temporal context
16:30 - 16:45	8.4	Fernández de Uña, Laura	Height-related sap-flow responses to VPD: a global-scale analysis of tree function under drought
16:45 - 17:00		Closing ceremony	

19:00 - 22:00 **Conference dinner** (Bürgerspital Weinstuben)



Preface

Dear colleagues,

We are happy to welcome you as participants of the 5th Xylem International Meeting at the University of Würzburg. Ecophysiological and ecological research has a long tradition at this university, which has been home to prominent figures such as Julius von Sachs, considered the father of experimental plant physiology, or Gregor Kraus, who played a foundational role in the fields of microclimatology and experimental ecology. Moreover, Würzburg's location in one of the most strongly heat- and drought-prone regions in Germany makes it a prime study site for plant drought responses. It is therefore an ideal location to continue the tradition of the Xylem International Meeting, which began in 2014 in Besse, France, and has since been hosted twice in Bordeaux, France, in 2015 and 2017 and once in Padua, Italy, in 2019.

With our diverse program comprising 54 oral and 60 poster presentations in a total of eight sessions covering topics from evolutionary history over variability in plant hydraulic traits, plant hydraulic models, peripheral hydraulics, concepts and methods, drought- and heat-induced tree mortality, xylem structure and function, and ecosystem water fluxes, we are confident that we cover a broad range of current topics related to the many aspects that make plant xylem such a fascinating research subject. We hope that this meeting will be a great opportunity to exchange knowledge, stimulate further collaboration and promote the work in our field.

We want to extend our gratitude to all the people that made this meeting possible, particularly the XIM Scientific Committee (José Torres-Ruiz, Sylvain Delzon and Hervé Cochard), the New Phytologist Foundation, Plant Biology and the German Society for Plant Sciences (DBG) for providing funding, Heike Kuhlmann, whose professional help with setting up the conference is highly appreciated, and the technical assistants, PhD and MSc students of the Department of Botany II of the University of Würzburg for their support.

We further wish to express our appreciation to the keynote speakers and chairs of our eight sessions as well as all presenters, without whose generous contribution this meeting could not take place in its present form.

After the pandemic impeded physical meetings for almost two years, being able to meet in person again is a wonderful opportunity to discuss our work with likeminded individuals in a setting that just cannot be replicated by virtual meetings. We are looking forward to a stimulating meeting in Würzburg!

Bernhard Schuldt

Roman Mathias Link

Pierre-André Waite

Excursions

Three different excursions are taking place on Thursday, September 22, that enable you to discover the picturesque historic city of Würzburg, learn about the the experiments conducted in the Bavarian State Research Center for Viticulture and Horticulture in Veitshöchheim, or travel to the Steigerwald Nature Park, where you can see the vertical structure of Central European broadleaved forest canopies on a 1,150 m long canopy walkway as well as strongly drought-affected forest sites.

To minimize delays, please be in time for the excursion you booked at the designated meeting place in front of the Residenz:

Excursion	Starting time	Meeting place
Historic City of Würzburg	10:00	In front of the Residenz
Bavarian Centre for Viticulture & Horticulture	09:00	In front of the Residenz
Steigerwald	08:00	In front of the Residenz

The meeting place is indicated on the map at the end of this booklet.



Top left: City of Würzburg (photo: Stadt Würzburg)
 Top right: Bavarian State Research Center for
 Viticulture and Horticulture (photo: P. Hönig, LWG)
 Bottom right: Steigerwald (photo:
www.baumwipfelpfadsteigerwald.de)

XIM5

Exhibitors

The following exhibitors can be found at the 5th Xylem International Meeting:



LI-COR, Inc.:
<https://www.licor.com/>



UP Umweltanalytische Produkte GmbH:
<https://www.upgmbh.com/>



UGT Umwelt-Geräte-Technik GmbH:
<https://www.ugt-online.de>



Heinz Walz GmbH:
<https://www.walz.com>

Keynote speakers

Prof. Dr. Jarmila Pittermann (Session 1: Evolutionary history)



Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California, USA

Jarmila Pittermann is a professor of plant biology at the University of California, Santa Cruz where she works on plant structure and function, particularly plant water transport in the context of ecology and evolution. She received her MSc at the University of Toronto and a PhD at the University of Utah where she examined the safety-efficiency trade-offs of conifer wood with respect to hydraulic efficiency and safety from hydraulic failure. Her current research focuses on the evolutionary ecophysiology of ferns and the drought performance of conifers in California's Sierra Nevada range.

Dr. José Alberto Ramírez-Valiente (Session 2: Variability in plant hydraulic traits)

Department of Forest Ecology and Genetics, Forest Research Centre (INIA, CSIC), Madrid, and Ecological and Forestry Applications Research Centre (CREAF), Barcelona, Spain

Jose Alberto Ramirez-Valiente is a researcher at the Centre for Research on Ecology and Forestry Applications (CREAF) in Barcelona. He defended his PhD on advanced forestry research at the Technical University of Madrid in 2010 with awards from the European Forest Institute and the Spanish Society of Forest Science. He then held different postdoctoral positions at the Australian National University, University of Minnesota, Doñana Biological Station and Spanish National Institute for Agriculture and Food Research and Technology.

Throughout his career, he has devoted his research to the study of phenotypic plasticity and intraspecific variation in functional traits and their role to cope with environmental heterogeneity and climate change in forest tree species. His research combines ecophysiology and quantitative genetics to understand how forest tree species adapt to the environment, their ability to respond to climatic changes and the influence of different evolutionary processes in shaping the levels of functional diversity observed in nature. More recently, he is focusing his research on the study of coordination of plant functions along resource-use availability gradients and the evolution of plant hydraulics at different organizational levels.



Dr. Hervé Cochard (Session 3: Plant hydraulic models)

INRA, PIAF, Université Clermont-Auvergne, Clermont-Ferrand, France

Hervé Cochard is an ecophysiologist and specialist in the circulation of xylem sap and the hydraulic functioning of trees. He has contributed to the development of new tools for measuring hydraulic characteristics and to the demonstration of the key role played by xylem hydraulic failure in plant mortality under extreme drought conditions. He is developing mechanistic models to predict tree water relations during extreme drought events. He is INRAE Research Director at the UMR PIAF in Clermont-Ferrand.



Prof. Dr. Rainer Hedrich (Session 4: Peripheral hydraulics)



Molecular Plant Physiology and Biophysics, Julius-von-Sachs-Institute for Biosciences, University of Würzburg, Germany

Rainer Hedrich, chair of Molecular Plant Physiology & Biophysics, pioneered the biology of plant ion channels. He introduced the patch clamp technique into the plant field by demonstrating for the first time the existence of plant ion channels. This discovery resulted in the elucidation of the structure-function relationships of plant ion channels, established the key role of ion channels in plants, and inspired the formation of a new research field, which is part of today's plant biology text books. This Würzburg lab made major contributions to uncover the functions of plant ion channels, co-transporters and pumps and showed crucial functions of these proteins for plant physiology and development. Using physiological and molecular-genetic analysis his lab revealed the voltage and pH sensor of plant potassium channels, uncovered their selectivity filters, demonstrated the interaction sites of important components to channel proteins and studied subsequent signaling events. He succeeded in reconstitution of the fast ABA signaling pathway of guard cells from receptor to anion channels activation, via protein phosphorylation, by using a drought stress protein kinase/phosphatase pair. Besides of basic research, the Würzburg lab contributed to the development of new model systems by elucidating the molecular basis of plant adaptation to dry, hot, and saline environments. Recently the Hedrich lab has show the carnivorous Venus flytrap is able to count electrical impulses.

Prof. Dr. Steven Jansen (Session 5: Concepts and methods)

Institute of Systematic Botany and Ecology, Ulm University, Ulm, Germany

Research activities of my lab at Ulm University focus on fluid transport in plants, with a special emphasis on functional anatomy of vascular tissues. We aim to address the longstanding question of how plants are able to transport liquids and gasses without seemingly much effort and a high energy demand. Current work includes: (1) the three-dimensional structure of bordered pits between water conducting cells and their function in fluid transport and embolism spread, (2) the functional role of insoluble, polar lipids and their link with nanobubbles in xylem sap, and (3) the dimensions and three-dimensional network of xylem conduits in roots, stems, and leaves. The anatomical methods applied include a wide range of imaging methods, including electron microscopy, X-ray tomography, and ptychography. Moreover, we apply ecophysiological measurements in the field and in the lab, as well as chemical analyses. Experimental work is conducted on forest trees, talking trees, and synthetic trees. While talking trees are equipped with various sensors to monitor traits related to growth and productivity (<http://svadss.org/svadss/uni-ulm/talking-tree/berti/>), synthetic trees represent evaporation-driven transport devices, aiming to provide optimal cooling and/or liquid transport under negative pressure without the aid of any fuel consuming pumps.



Prof. Dr. Charlotte Grossiord (Session 6: Drought- and heat-induced tree mortality)

Plant Ecology Research Laboratory (PERL), School of Architecture, Civil and Environmental Engineering (EPFL) and Functional Plant Ecology, Community Ecology Unit, Swiss Federal Institute for Forest, Snow and Landscape (WSL), Lausanne, Switzerland



How does global warming affect plants – and thus the important functions and services provided for humans by ecosystems? Charlotte Grossiord, an ecophysiolgist at EPFL/WSL, has been investigating this question throughout her entire scientific career. Her research spans from biodiversity impacts on ecosystem functioning to understanding climate impacts on survival and mortality of trees. Charlotte's research has made great steps forward in our understanding of plant responses to extreme conditions and on the significance of species interactions in forests. In her doctorate at Lorraine University and INRA-Nancy in France, she explored how tree species diversity affects the water balance of trees. She focused in particular on the resistance of plants to extreme events. In her PostDoc at the Los Alamos



National Laboratory in the USA, Charlotte Grossiord investigated how forests adapt to the exacerbation of droughts with higher temperature. To continue and expand her research on these topics, EPFL and WSL have jointly appointed her tenure-track assistant professor in March 2020.

Dr. Andrew J. McElrone (Session 7: Xylem structure and function)

Department of Viticulture and Enology, University of California and USDA-ARS, Crops Pathology and Genetics Research Unit, Davis, California, USA

Dr. Andrew McElrone is a Research Plant Physiologist with USDA-ARS, an adjunct faculty member in Viticulture and Enology at UC Davis, and served as the Acting Director of the USDA California Climate Hub. For over two decades, he has studied plant responses to changing environmental conditions in agricultural and natural ecosystems, and has become an internationally recognized expert in plant water use and responses to drought with specific applications to irrigation management and sensor technology development. His research program is screening woody perennial crops for improved drought tolerance, developing efficient genotype-specific irrigation strategies, and advancing new technology to better quantify crop water use and stress with proximal and remote sensors. Along with collaborators, he pioneered the use of x-ray microCT for studying plant water uptake and transport processes at Lawrence Berkeley National Lab's Advanced Light Source. As a collaborator and lead on the GRAPEX and T-REX projects (Grape Remote sensing and Atmospheric Profiling and Evapotranspiration eXperiment; Tree crop Remote sensing of Evapotranspiration eXperiment), he is helping to ground truth crop ET and stress estimates via soil moisture sensing, leaf and whole plant physiological measurements, and ecosystem fluxes. Prior to his current position, Dr. McElrone studied water use in deep tree roots using caves (~20 meters below ground) and examined plant- and pathogenic-response to changing atmospheric conditions—both as a post-doctoral researcher at Duke University and an assistant professor of biology and environmental science at Saint Joseph's University in Philadelphia.





Oral presentations

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Session 1-O0 - Evolutionary history

Xylem attributes shaped the evolution of Eupolypod ferns

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The Cretaceous expansion of angiosperm-dominated tropical forests created abundant habitat space in the canopy. This is a stressful niche, however, because the epiphytic plants that occupy branches and tree trunks must contend with sunnier, less nutrient-rich, and often drier conditions. Despite these challenges, several plant lineages, including orchids and bromeliads, adapted to the epiphytic niche during the Cenozoic by evolving water-absorbing roots, high leaf capacitance, and the ability to store water in rosette water tanks. Interestingly, ferns also speciated and radiated into the canopy, although the physiological means by which this was achieved are not fully understood. Ferns are developmentally and physiologically canalized relative to angiosperms raising the question of what the key trade-offs may have been to support their climb to the canopy. My talk will examine the water relations, and xylem structure and function of these seedless vascular plants through the prism of deep-time evolution, using this opportunity to highlight some of the methodological complexities that can arise when working with non-woody taxa. Indeed, there is much that the fern morphospace can reveal about the adaptive priorities of all plants that evolved to contend with stressful habitats.

Session 1-O1 - Evolutionary history

Co-evolution of axial parenchyma and vessels in relation to water transport in woody angiosperms reveals coordinated functional adaptation to climate across biomes

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Wood parenchyma plays crucial roles in maintenance of woody plants. Functions range from storage and transport of metabolites and solutes to defence and maintenance of the plant hydraulic system. Ray and axial parenchyma (RAP) are oriented 3-dimensionally in radial and axial files. RP forms a two-way transport network connecting inner-bark to wood while AP forms a vertically-oriented support-link to the vessels, dead conduits that transport water under negative pressure. Although this anatomically and functionally integrated coupling between AP and vessels has been shown, we have yet to understand the evolution driving this coordination, which is related to how phylogenetically conserved vessels, ray and axial parenchyma are within clades. We tested hypotheses with a dataset of 2,332 globally distributed species by comparing the performance of pure drift, Lambda effect and Brownian motion models of trait evolution with the selection-inertia, Ornstein-Uhlenbeck model. Phylogeny confirms that the proportion, spatial arrangement of AP and ultimately the level of support to vessels was found to co-evolve with vessels, which, in turn, is related to climate and maximum plant height as a coordinated assemblage; RP was found to be independent of climate. Highest evolutionary rates were found in AP and maximum plant height, while vessels were more conserved among clades. We provide further evidence to support the role of axial parenchyma in long-distance water transport, facilitating co-optimisation of hydraulic efficiency and safety in angiosperm woody plants.



Session 1-O2 - Evolutionary history

Evolution of xylem vulnerability to cavitation in cereal crops: the downside of domestication and selection in wheat (*Triticum* sp.)

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Increasing warmer and drier conditions underlying climate change are threatening global crop production. Plant productivity depends on the efficiency of the water transport system, thus assessing the extent to which the hydraulic system of cereal crops can withstand drier conditions is crucial to evaluate their capacity to cope with changing environmental conditions. We characterised xylem vulnerability to cavitation within wheat phylogeny, including wild and cultivated lines, and in a pool of common wheat (*Triticum aestivum*) cultivars bred for contrasting growing environments. We provide strong evidence that domestication promoted the development of a weaker hydraulic system in cultivated lines, and particularly in the major wheat species, *T. aestivum*. We show an important variability in vulnerability to cavitation in this latter wheat species, yet the more resistant genotypes were surprisingly not associated with drier growing conditions. Together these results prove that human actions shaped the recent evolution of wheat hydraulic system, through the selection of production-related traits. We emphasize the need to further explore key hydraulic traits involved in drought response in crops and how they relate to other physiological traits to better understand drought resistance in cultivated plants.



Session 1-O3 - Evolutionary history

Drought triggered woodiness on islands worldwide

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Insular woodiness (IW) - the evolutionary transition from herbaceousness towards woodiness on islands - is one of the most iconic features of island floras. Since pioneering work by Darwin, a number of drivers of insular woodiness have been proposed: increased competition, favourable aseasonal climate, lack of large native herbivores, and drought. However, information on the occurrence of IW is fragmented, hampering tests of these potential drivers. Here, we identify 1,097 insular woody species on 375 islands, and infer at least 175 evolutionary transitions on 31 archipelagos, concentrated in six angiosperm families. Structural equation models reveal that the insular woody species richness on oceanic islands correlates with favourable aseasonal climate, followed by increased drought and island isolation (approximating competition). When continental islands are also included, reduced herbivory pressure by large native mammals, increased drought and island isolation are most relevant. This means that drought - defined in the model by precipitation warmest quarter, precipitation seasonality and aridity index - is one of the main drivers of IW across islands worldwide. This drought hypothesis has already been confirmed by case studies showing a positive correlation between increased embolism resistance and increased stem woodiness/lignification in a number of plant lineages. We will discuss how this increased woodiness/lignification and co-evolving anatomical traits such as increased intervessel pit membrane thickness contribute to reduced embolism vulnerability.



Session 1-O4 - Evolutionary history

Drought resistance as a primary driver of stelar evolution in early vascular plants

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The earliest vascular plants had developed a cylindrical and centrally located stele containing a xylem strand surrounded by phloem by the Late Silurian period (~420mya). This simple form soon diversified into more complex morphologies as both the size and complexity of the plant body increased. Current hypotheses surrounding stelar evolution suggest this complexity was developmentally linked to increasing ramification of the plant body, but no selective pressure explaining increasing stelar complexity has been found. Here, we show that topological changes in the xylem conduit network lead to progressively greater drought resistance as stele morphology diverges from the simple ancestral form. The mean number of xylem conduit neighbours decreases and pathways for drought-induced embolism spread become increasingly concentrated in fewer, more central conduits in the stele. These topological effects continuously increase the drought intensity threshold for mortality through xylem dysfunction as the complexity of the xylem strand shape increases, providing a selective pressure to explain observed trajectories of stelar evolution in the fossil record and the diversity of extant stelar shapes. Known links between stelar morphology and plant body construction as well as our new results suggest that selection for drought resistant xylem networks may have played a larger role in the evolution of overall land plant body plans than has been hitherto appreciated.



Session 1-O5 - Evolutionary history

Rehydration dynamics via aerial surfaces – a mechanistic and evolutionary approach

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The absorption of water through green, aerial surfaces of plants, generally referred to as foliar water uptake, is a widely spread phenomenon, yet the underlying mechanisms and biological implications are unclear. We aim to describe some recent advances in our understanding of this water pathway. From a mechanistic viewpoint, the determination of hydraulic parameters such as the resistance to water flow over time and rates of absorption revealed a dynamic control of the process by the cuticle and are consistent with the absorption of water vapor through stomata. We are currently analyzing the dynamics of rehydration of aerial plant parts across phylogeny (60-70 taxa) for two hydraulic pathways, the vasculature or, in the case of non-vascular plants, internal diffusion, and the vasculature. Preliminary data suggest the presence of a tradeoff between the capacity to rehydrate via internal tissues and the aerial surface, with the evolution of the vasculature setting a milestone in such capacity. There is, however, not a simple binary switch between a bryophytic and tracheophytic mode of surface rehydration. In this regard, ferns and monocots attained a relatively high capacity to rehydrate via the surface (average time constants of ~3 and ~4 h, respectively, vs ~1 h for mosses and ~7 h for other angiosperm classes, or ~9 for *Ginkgo*). The results obtained from this first broad phylogenetic survey provide insight into the evolutionary significance of the foliar water uptake pathway.



Session 2-O0 - Variability in plant hydraulic traits

Phenotypic plasticity of hydraulic traits in a global change context

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Predicting plastic responses in traits important for fitness is essential to improve our understanding of plant species potential to face global change. In this talk, I will review the main findings on phenotypic plasticity in hydraulic traits and will synthesize the results from a global meta-analysis evaluating plastic responses across different traits, species and environmental conditions. I will show that most species exhibit some level of plasticity in hydraulic traits, but its magnitude is remarkably lower in hydraulic safety traits. Differences among evolutionary groups are apparent with gymnosperms presenting higher resistance to embolism (P_{50}) but lower plasticity than angiosperms, which suggests a trade-off between resistance to embolism and its plasticity. In general, sapwood area/leaf area ratio increases and P_{50} , wilting point and hydraulic conductivity (K_s) decrease under dry conditions. In fact, the plastic responses of P_{50} and K_s are strongly associated at intra-study level, indicating that species reducing P_{50} also reduce K_s . Finally, I will highlight the strong bias in the literature towards studies evaluating plasticity in response to water availability, and I will point out that hydraulic traits also exhibit pervasive plastic responses to other environmental factors that deserve deeper attention.

Key message: Plastic responses are strongly trait-, environment- and species-dependent, but in general, resistance to embolism has low plasticity, particularly in gymnosperms, and in response to drought, it commonly involves changes in xylem hydraulic efficiency.



Session 2-O1 - Variability in plant hydraulic traits

The global vulnerability of plant xylem

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More than just a scaffold, xylem conduits deliver the water necessary for reproductive and metabolic processes, importantly including turgor maintenance—and with it, the form and function of more than 300,000 plant species globally. Across these many species, the anatomy, physiology, and structural roles of xylem is highly varied. Xylem's importance extends far beyond plants, as vegetated terrestrial biomes are hosts to most of Earth's biodiversity, and plant transpiration accounts for more than 80% of all terrestrial evaporation. Xylem's function underpins innumerable, complex processes. Yet, its vital



role in supporting global biodiversity, and fluxes of both water and carbon, is tenuous, and the impairment and eventual failure of xylem can result in devastating consequences for plants and plant-dependent life. Here, we present the xylem functional traits database (XFT), an interactive web application hosting the world's largest set of observations for xylem vulnerability, with over 4,500 unique observations. Geographically, our database contains observations on six continents. Taxonomically, the XFT covers Pteridophytes, Gymnosperms, and Angiosperms, with observations of xylem vulnerability for ~1,570 species, 723 genera, and 166 families. Climatically, xylem vulnerability has been measured in plants growing across gradients of 30°C of mean annual temperature, and 4 meters of mean annual rainfall. Yet, major biases and gaps across space, climate, and growth forms limit our understanding of xylem vulnerability. We outline critical next steps to further understanding the global vulnerability of plant xylem.

Session 2-O2 - Variability in plant hydraulic traits

Long-term acclimation to soil moisture regulates thresholds of photosynthesis and thermoregulation capacity of *Pinus sylvestris*

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Drought-induced hydraulic failure and increased Vapor Pressure Deficit (VPD) are some of the main drivers of forest mortality globally. Unmanned aerial vehicles (UAVs) can assess canopy temperature over large areas. Under water-stressed conditions, trees close their stomata, which results in lower transpiration rate and heat dissipation. Thus, high leaf temperature is often the signal of drought stress in trees. Mapping leaf thermal signature in forest ecosystems can provide important insight into management strategies under global warming.

Using a field-based irrigation experiment with *P. sylvestris*, we determined how long-term acclimation to changing soil moisture affects the water use sensitivity of trees to soil and atmospheric droughts and its feedback to canopy temperature regulation.

Under warmer weather (i.e., at midday or in the middle of the growing season), we found that irrigated trees reached higher leaf temperatures compared to control trees. Higher leaf temperature resulted from a premature stomatal closure and reduced transpiration to avoid xylem cavitation. This was supported by a steep decrease of stomatal conductance and water potentials observed in irrigated trees in early afternoon or during the summer.

Key message: Our work highlights that long-term acclimation to reduced soil moisture allows a sustained water-use during hot periods in order to maintain foliar temperature within an optimum range for photosynthesis.



Session 2-O3 - Variability in plant hydraulic traits

Inter- and intra-specific variation among tree populations in their vulnerability to drought across a rainfall gradient in Puerto Rico

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Climate change is increasing the duration and frequency of drought events impacting forests worldwide. Variation in hydraulic traits among (interspecific) and within (intraspecific) species has important consequences for determining population-level response to drought. We examined how hydraulic traits linked to drought avoidance (leaf, stem capacitance) and tolerance (turgor loss point, embolism resistance, and safety margins), vary along a pronounced rainfall gradient (950–3,500 mm yr⁻¹) across Puerto Rico to address: How do these traits vary at the regional level (across the island), site-level (interspecific), and species-level (intraspecific)? At six sites with distinct rainfall, we measured hydraulic traits on a total of 283 trees belonging to 20 different species. We measured as many of the 20 target species as possible at each of the six sites resulting in 4 to 13 species at each location. Across a declining rainfall gradient, we found an overall decrease in drought avoidance and an increase in drought tolerance. At the forest level, sites with higher rainfall had hydraulic traits associated with greater drought avoidance and drier sites with greater drought tolerance. For five species, we found intraspecific variation—individuals in the drier sites had greater embolism resistance. For example, *Tabebuia heterophylla*, had $P_{50} = -3$ MPa at the wetter site and $P_{50} = -5$ MPa at the drier one. We conclude that wetter forests employ more drought avoidance strategies and drier sites more drought tolerance and that intraspecific hydraulic variation contributes to this pattern.

Session 2-O4 - Variability in plant hydraulic traits

Understanding the effects of acclimation to water deficit on the internal water storage dynamics of *Populus tremula* x *alba* during extreme drought

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Internal tree water storage plays an important role in water regulation and is crucial for survival during drought. Indeed, its buffering impact on transpiration-induced fluctuations in xylem pressure is critical in avoiding large decreases in xylem pressure and uncontrolled embolism. Studies show that the ability of trees to acclimate hydraulic and morphological traits determines its capacity to tolerate and survive increasing drought. However if the plasticity in cavitation resistance traits is commonly studied (P_{50} , g_{min}), little is known about the effect of the acclimation to water deficit on internal water storage dynamics of tree.

Young poplars were grown in contrasted water availability in order to induce acclimation in hydraulic properties. Then, they were exposed to a progressive drought. Dendrometers were installed to monitor the variations in diameter. We characterized the evolution of maximum daily shrinkage and the percentage loss of diameters for the different conditions during the drought period. Water potential and stomatal conductance have been assessed throughout the drought. When targeted physiological stages were reached, samples were collected and physiological traits like percentage loss of conductivity, relative water content and electrolyte leakage were measured. Trees were then rehydrated in order to analyze their recovery capacity.



Session 2-O5 - Variability in plant hydraulic traits

To everything there is a season, including xylem vulnerability

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Cavitation resistance is considered a static trait, probably because the xylem is composed of dead cells and is thus less plastic once formed. At the same time, there are good reasons to assume that cavitation resistance is dynamic, as many hydraulic traits will change during the season. We hypothesized that the xylem vulnerability is a seasonally plastic trait, adjusting to lower water potential (Ψ_x) along summer in coordination with the turgor loss point ($\Psi_{t\text{lp}}$). We examined the seasonal dynamics of the Ψ_x , $\Psi_{t\text{lp}}$, and cavitation resistance in leaves of ten deciduous species from different habitats and in stems of *Pinus halepensis* under Mediterranean climate. We found that the cavitation resistance, in terms of P_{50} (the xylem pressure that leads to 50% cavitation), is a seasonally plastic trait in the five deciduous species from Mediterranean habitat, and in two out of the five species from subtropical or tropical habitat. The seasonal shift ranged from 0.7 MPa in *Vitis vinifera* and up to 2.5 MPa in *Celtis australis*. Also, the stems *Pinus halepensis* decreased their P_{50} by 1 MPa from the end of the wet season to the end of the dry season in coordination with the dynamics of the Ψ_x and the $\Psi_{t\text{lp}}$. The observed plasticity enabled the plants to maintain a stable positive hydraulic safety margin and avoid cavitation during the long dry season. Seasonal plasticity is vital for understanding the actual risk of cavitation to plants and for modeling species' ability to sustain harsh environments.

Degree of isohydry in mature European beech and Norway spruce and strategy adjustments under repeated summer drought

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Plant species show diverse responses to drought stress, depending on their degree of isohydry. Rather anisohydric plants risk hydraulic failure by keeping their stomata open even at low water potentials to continue taking up CO₂. More isohydric species close their stomata early under drought to minimize water loss, at the expense of very low to no CO₂ uptake. However, the drought response patterns are much more sophisticated and might differ among tree structures. Here we show the responses in terms of hydraulic vulnerability, pre-dawn/minimum water potential and stomatal conductance of mature European beech (*Fagus sylvatica* (L)) and Norway spruce (*Picea abies* Karst(L)) to repeated drought induced by throughfall exclusion over five growing seasons. Under control conditions, spruce tends to react more isohydric than beech. Under drought, both species showed similar acclimations in branch xylem vulnerability (i.e. shifts towards more negative $\Psi_{12/50/88}$), and leaf turgor loss point and osmoregulation. However, the stomatal control revealed a pronounced shift towards a more isohydric behavior in spruce, whereas only a limited acclimation in beech towards a more anisohydric behavior under drought was found. Additionally, the safety margin between stomatal closure and embolism formation was significantly increased in spruce, while beech simply maintained its safety margins.

Key Message: Both species adjusted their degree of isohydry under repeated drought by enforcing their respective strategy, with spruce reacting stronger than beech.

Session 2-O7 - Variability in plant hydraulic traits

Hydraulic strategies of two woody Mediterranean species are dynamic

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Knowledge of plant hydraulic strategies is crucial to understand the responses of plants to increasing drought under climate change. Recent advances indicate that hydraulic strategies are more dynamic than assumed and can be influenced by a variety of abiotic factors other than soil water resources, such as vapour pressure deficit. However, the influence of biotic factors, such as plant competition on hydraulic strategies (i.e. isohydricity) has rarely been considered. To test the influence of both, abiotic and biotic factors on hydraulic strategies, we implemented a combined shrub invasion (*Cistus ladanifer*) and rain exclusion experiment in a Mediterranean cork oak (*Quercus suber*) ecosystem including two woody species with contrasting drought adaptation strategies. By assessing the response of the minimum leaf water potential at midday to declining pre-dawn leaf water potentials, we demonstrate that both investigated species shifted their isohydricity from wet to dry phases in response to seasonal abiotic conditions. Intriguingly, *Q. suber* under *C. ladanifer* invasion revealed a modified hydraulic strategy compared to non-invaded trees independent of the rain exclusion in dry phases. This modified isohydricity was accompanied by lower tree water fluxes and stomatal conductance, as well as reduced leaf area and decreased stem growth, pointing towards a lower carbon assimilation.

Key message: Our results demonstrate that the interplay of species-specific hydraulic traits and their abiotic and biotic environment dynamically determine the hydraulic strategy of plants.



Session 3-O0 - Plant hydraulic models

Trait-based modeling of plant hydraulics

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Drought-related tree mortality events have been increasing globally for the past few decades and it is feared that this situation will worsen with the increasing risk of heat waves. Understanding the physiological basis of these die-offs can help identify better adapted species or genotypes, but can also improve predictive models of these mortality risks. A drought modifies the hydric and hydraulic functions of a tree, and this more so the more intense the drought is. Beyond a certain intensity, embolism events can occur in the xylem vessels, which can lead to desiccation and then death of the crowns. Vulnerability to embolism thus appears to be a key physiological process in the mortality of plants exposed to drought. It has been studied in detail since the 1980s and work is currently focused on the concept of hydraulic failure risk. This risk integrates the intrinsic vulnerability of the xylem to embolism, but also the water stress undergone by the trees during drought. It is mainly the residual cuticular transpiration of the tree that determines the rate of dehydration and thus the risk of embolism. To assess this risk, all of these physiological processes must be integrated into a model of tree water and hydraulic functioning. The predictions of such models illustrate the key role of xylem vulnerability to embolism and cuticular losses in the mortality process. In particular, a high risk of embolism exists when leaf temperature passes a critical threshold, which could explain the aggravating effect of heat waves. Moreover, the model predicts a very strong increase in the risk of embolism with global warming, and the genetic variability and phenotypic plasticity of forest species seem too low to limit this risk.



Session 3-O1 - Plant hydraulic models

Assessing the vulnerability of forest ecosystems to drought and fire with the plant-hydraulics model *SurEau-Ecos*

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Widespread increases in drought-induced tree mortality and wildfire danger have been observed around the globe and these trends are likely to continue because of ongoing climate change. This raises the need to identify the mechanisms and conditions that drive the desiccation of forest ecosystems and identify regions and species that are likely to experience the most frequent and significant damages. We developed the trait-based, plant hydraulics *SurEau-Ecos* model to simulate plant water status at scales from stand to region. The water fluxes from the soil to the atmosphere were represented through two plant organs (a leaf and a stem, which includes the volume of the trunk, roots and branches) as the product of an interface conductance and the difference of water potentials. Each organ was described by its symplasmic and apoplasmic compartments. The dynamics of plant's water status beyond the point of stomatal closure were explicitly represented via residual transpiration flow, plant cavitation and solicitation of plants' water reservoirs. We further embedded a fuel moisture content module into *SurEau-Ecos* to simulate fuel moisture by explicitly taking into account the impact of mortality on forest flammability. We present here several applications and results obtained with *SurEau-Ecos* and discuss the implications of our findings for our understanding of forest vulnerability to drought in a warming world.



Session 3-O2 - Plant hydraulic models

Interspecific variability in physiological thresholds during dehydration reveals contrasting drought-response strategies and vulnerability to hydraulic failure in rainforest tree saplings

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Hydraulic traits related to the ability of plants to tolerate and avoid the effects of dehydration represent key mechanisms influencing specie's survival during drought. However, little is known on how they shape multidimensional plant drought-response strategies and how important they are for survival, especially in tropical rainforest trees. Much focus has been made on hydraulic traits related to the ability of trees to avoid reaching critical levels of xylem embolism, since hydraulic failure is regarded as an ubiquitous process leading to drought-induced mortality. Less attention has been given to the potential simultaneous role of non-structural carbohydrates (NSC), which could get depleted during drought and help maintain osmoregulation. In this study, we have characterized the diversity of drought-response strategies in 12 rainforest tree saplings by measuring leaf turgor loss point, leaf and stem xylem vulnerability to embolism, lethal levels of water potentials and associated losses in hydraulic conductance causing mortality, as well as minimum leaf conductance. We then evaluated whether these strategies determined the response of NSC storage and use as well as the prevalence of hydraulic failure and/or carbon starvation across species during an imposed severe drought. Finally, in order to test the importance of traits related to survival during drought, we applied SurEau, a mechanistic model computing time to hydraulic failure. This talk summarizes the main findings of this study, underlining specificities in plant drought-survival across tropical rainforest tree species.



Session 3-O3 - Plant hydraulic models

Time to die: multilevel coordinated response and desiccation time during drought of 12 temperate tree species

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The observed rise in atmospheric water stress is threatening Central European forests, highlighting the need for a precise characterization of the drought tolerance of co-occurring temperate tree species. We characterized the drought performance for the saplings of 12 temperate coniferous and broadleaved tree species using a set of new methods to estimate key hydraulic traits. Among others, these include leaf phenology, water potentials at turgor loss point (P_{tlp}), stomatal closure (P_{st}) and the three measures of xylem safety (P_{12} , P_{50} and P_{88}), shoot capacitance and relative water content at critical hydraulic thresholds, as well as cuticular (g_{min}) and bark conductance (g_{bark}). We will use some of those variables to estimate species desiccation time during drought (t_{crit}), i.e. the time it takes to reach critical xylem thresholds after stomatal closure. Additional dry-out experiments will reveal whether the model developed by Blackman and colleagues is suited to predict desiccation time of temperate coniferous and broadleaved tree species. Finally, we will relate t_{crit} to available drought tolerance indices of these species, considering differences in their hydraulic strategies. We consider this a major step towards the identification of drought tolerant tree species suited for our future forests.



Session 3-O4 - Plant hydraulic models

Modelling the cycles of winter stem pressure in walnut tree

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Frost hardiness is the main factor affecting plant species distribution at high latitudes and altitudes. The main effects of freeze-thaw cycles on trees are damages to living cells, as well as the formation of gas embolism in xylem vessels, thus blocking sap flow in spring. The effect of frost on trees can be quantified through changes in branch diameter.

In order to resorb embolism, some species (walnut, maple, birch, etc.) exhibit an increase in the xylem sap pressure during successive freeze-thaw cycles, which leads to the exudation of sap after pruning. The multiplicity of relevant scales (spatial and temporal), the presence of water simultaneously in gaseous, liquid and solid form, as well as the corresponding phase changes, bring complexity into the modelling of these phenomena.

In this work, we present a numerical model coupling heat transfer, phase change, water and osmotic fluxes, taking into consideration different cell types within walnut branch tissues. We show how diameter and pressure variations are inter-related, and we validate the model against experimental results from the literature. We eventually show how this work can be adapted to other types of anatomical structures and to other environmental conditions, in order to explore inter-species differences.

Session 3-O5 - Plant hydraulic models

Evaluating the plant and soil limitation to root water uptake using thermodynamics

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Root water uptake has been studied extensively to understand transpiration. Many of those studies consider hydraulics, in that they model the water flow from the soil through the plant into the atmosphere. One important question is how to identify the bottle necks along the flow paths and whether and where they lie within the plant or soil?

Here, we propose a thermodynamic formulation of water flow and soil water retention to assess losses along the flow path. It separates the energy exported at the root collar into losses within different realms, and allows ranking impediments.

The application of this approach to a complex 3-dimensional root water uptake model reveals insights on the role of root versus soil resistances to transpiration. We compare the efficiency of root water uptake in root systems with varying portion of uptake and transport roots but similar root length, branching and total uptake. We only model unlimited transpiration. The results show that uptake and the least negative potential is afforded by heterogenous root systems, with many acting near the optimum. A great loss of efficiency only occurs in the extreme cases (only uptake or only transport roots). In systems near the optimum, abiotic factors become the dominant impeding factor to uptake when the soil dries, leading to exponential drop of the xylem potential. Both soil water retention or soil water flow can be the cause, depending on the soil type.

Our results underline the substantial flexibility of hierarchical networks, such as root systems, and the importance of soil properties for root uptake.

Session 4-O0 - Peripheral hydraulics

New insight in to guard cell networks controlling stomatal action

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Ca²⁺ signals play a special role in guard cells, as these signals can be directly translated into movement of stomatal pores that control leaf transpiration. The stomatal aperture is controlled by volume changes in pairs of guard cells that surround the stomatal pore. Studies in the late 1980ies and early 1990ies, provided two lines of evidence that Ca²⁺ signals are important for stomatal movements: i) patch-clamp experiments revealed that guard cell anion channels, which are crucial for stomatal closure, are activated by elevated concentrations of cytosolic Ca²⁺ and ii) studies with fluorescent Ca²⁺ reporters showed that stomatal closure, induced by the stress hormone ABA, can trigger Ca²⁺ signals in guard cells. Later studies showed that such Ca²⁺ signals can also be evoked in guard cells by other stomatal closing signals such as high CO₂ concentrations, darkness, and pathogen-related molecules. Thus, Ca²⁺ signals play a general role in the regulation of guard cell ion fluxes, turgor and volume changes and consequently control stomatal movement.

The question remains; how efficiently are cytosolic guard cell Ca²⁺ signals in provoking stomatal closure? So far, this question was addressed by rapid changes in the composition of the extracellular solution. However, these approaches had the disadvantage that manipulation of the guard cell plasma membrane potential inevitably will have a direct impact on ion transport and stomatal movement. We therefore explored alternative approaches to evoke defined cytosolic Ca²⁺ signals in guard cells by a Ca²⁺ permeable ChannelRhodopsin Ca²⁺-CHR. Activation of Ca²⁺-CHR in guard cells, with short pulses of light, caused “Ca²⁺ sparks” that triggered prolonged calcium transients, through Ca²⁺-induced Ca²⁺-release (CICR). Stomata could be completely closed within 10 min, showing that optogenetically imposed Ca²⁺ signals can be used to control and thereby decompose the mechanisms underlying stomatal action.



Session 4-O1 - Peripheral hydraulics

Does xylem cavitation lead to foliar catastrophe?

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Catastrophic damage to plant vascular systems is widely viewed as a primary driver of accelerating global forest mortality associated with increasing drought and heat. However, causality has never been demonstrated between cavitation in the vascular system and tissue death in plants. Testing this fundamental assumption, the water content in leaves and whole plants of wilted tomato mutants was manipulated while simultaneously tracking xylem network cavitation *in situ* and in real-time. Our results reveal a precise spatial and temporal linkage between cavitation in the leaf vein network and damage to downstream photosynthetic tissues. The unambiguous connection demonstrated here between vascular cavitation and leaf tissue damage highlights the importance of stomatal regulation of transpiration to prevent lethal xylem cavitation in leaf tissue.



Session 4-O2 - Peripheral hydraulics

Leaky leaves: the importance of g_{\min} in determining time to death in wheat under drought

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More frequent droughts and rising temperatures pose serious threats to agriculture and global food production. The capacity of crops, such as wheat to grow under increasingly unfavourable conditions are determined by hydraulic and morphological traits that allow plants to tolerate water-scarcity and delay mortality, while enabling grain production.

Traditional breeding for drought resistance often focuses on selecting for varieties with improved water-use efficiency whilst little is known about the potential of other traits to improve drought resistance.

The large diversity in wheat genotypes, provides a unique opportunity to explore combinations of drought-tolerance traits, such as stomatal closure, leaf residual conductance (main source of water loss in leaves after stomatal closure; g_{\min}), leaf hydraulic vulnerability (P_{50}) and their relative importance in delaying hydraulic failure and improving grain production.

A range of hydraulic and drought-adaptive traits were measured in common wheat cultivars, with these varieties then subjected to lethal drought. The time for plants to dry-down to critical levels of water stress was significantly determined by the continued loss of water from leaves after stomatal closure. Plants with low rates of g_{\min} survived for up to twice as long under severe water-limitation as genotypes with high rates of g_{\min} . g_{\min} was also found to acclimate to growth conditions.

Large genotype differences in g_{\min} and its influence in time to drought-induced death suggest that manipulating this trait could enable the development of more drought-tolerant crops.



Session 4-O3 - Peripheral hydraulics

Leaf dehydration dynamics after stomatal closure, from non-vascular plants to angiosperms

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During drought events, it is beneficial for plants to close stomata to prevent water loss. Yet, plants are not perfectly hermetic after stomatal closure, and water loss continues through leaky stomata and the leaf cuticle. Such residual conductance, known as minimum conductance (g_{\min}), is highly relevant since it informs on the water depletion dynamics under severe drought stress. We characterized leaf dehydration dynamics of c. 100 species with a high phylogenetic and ecological diversity, from mosses to flowering plants. We observe that residual conductance is highly variable during leaf dehydration, and we set up a novel method to have reliable estimations of g_{\min} based on relative water content boundaries and physiologically relevant thresholds. We shed light on the evolutionary and ecological significance of g_{\min} variation, highlighting the influence of phenology and growth form on dehydration dynamics across plant clades. We show that deciduous species have higher residual conductance than evergreen species, which have superior capacities to withhold water during drought. Likewise, residual conductance values differ across growth forms, with herbaceous leaves showing higher g_{\min} than those of woody species. Finally, we explore the relationship of g_{\min} with stomatal and epidermal features in order to explain the structural mechanisms promoting water retention during drought stress.



Session 4-O4 - Peripheral hydraulics

The importance of stomatal closure in preventing embolism

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Stomatal closure is essential in preventing embolism formation during drought. The driver of stomatal closure during drought remains unknown, furthermore the diversity of strategies that prevent embolism during drought in a forest remain understudied. Here we measured leaf embolism resistance, leaf gas exchange, foliage abscisic acid (ABA), non-structural carbohydrate and chlorophyll levels through a growing season in four species occupying a temperate deciduous forest understory, and in a neighbouring 80% rainfall exclusion plot. We observed a high diversity of strategies in our sampled species that prevented embolism formation during drought. In the insidiously invasive *Lonicera maackii*, leaves were highly embolism resistant, such that water potentials during drought remained at least 1 MPa higher than the threshold of incipient embolism. In the tree *Ulmus rubra* and monocot *Smilax tamnoides* ABA was synthesized during seasonal drought, closing stomata and preventing water potentials from declining to a threshold at which embolism formed. In contrast, in the tree *Celtis occidentalis* ABA was not synthesized as leaf water potentials declined during a seasonal drought; consequently, stomata did not close, water potentials declined to levels that triggered at least 50% embolism formation, and leaves were shed. We show that the synthesis of ABA is critical for the prevention of embolism formation during seasonal drought in the understory, and that highly resistant xylem may enhance invasiveness by preventing the inhibition of gas exchange during seasonal drought events.



Session 4-O5 - Peripheral hydraulics

The point of non-recovery of leaf photosynthetic activity and gas exchanges is determined by the spread of cavitation in leaf minor veins

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To understand the climatic drivers of canopy collapse in forest ecosystems, the mechanism that triggers leaf damage and prevents recovery to drought is needed. Plants of *Eucalyptus viminalis* were subjected to cycles of severe water stress and recovery to investigate the recovery potential of photosynthetic activity and gas exchanges after rewatering. The thresholds of water stress at which the plants were exposed corresponded to water potentials associated with leaf cavitation (from 0 to 100%), thus linking the role of leaf hydraulic failure in preventing the recovery of the photosynthetic tissue. We found that despite a total recovery in stem water potential, once cavitation spread in the minor vein order, photosynthetic activity and gas exchanges did not recover upon rehydration. However, partial cavitation in the redundant vein orders (midrib and major veins) allowed partial recovery of gas exchanges. This study highlights the fundamental role of minor veins in determining the point of leaf irreversible damage during water stress.

Key message: The point of non-recovery in photosynthetic activity and gas exchanges of leaves subjected to water stress is determined by cavitation spread in the minor vein order, which caused leaf irreversible damage.

Session 4-O6 - Peripheral hydraulics

Tree water loss through bark in dry conditions

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Tree bark has static pores, lenticels that intersperse the bark and allow exchange of gases between the stem and ambient air. To prevent excess water loss, plants typically close their stomata before massive embolism formation occurs, but unregulated water loss through leaf cuticles and bark lenticels continues after stomatal closure. We studied the dynamics of bark transpiration and its role in whole tree water loss in *Pinus halepensis* growing in dry conditions by running continuous measurements (6 months) of water loss from branch segments and needle-bearing shoots in a control and an irrigation plot in Yatir forest, Israel. The results show that transpiration rate per bark area was typically ~76% of the shoot transpiration rate (on projected shoot area basis). Irrigation of trees did not affect bark transpiration rate, whereas shoot transpiration was greatly increased due to stomatal control. Bark transpiration was estimated to account for ~70% of total tree water loss in drought-stressed trees, but only <10% of total tree water loss in the irrigated trees because of the difference in stomatal control.

Key message: Our results demonstrate that although bark transpiration represents a small fraction of the total water loss through transpiration from foliage in non-stressed trees, it may have a large impact during drought.



Session 4-O7 - Peripheral hydraulics

Soil drought has a more decisive impact than temperature on leaf hydraulic traits during hot droughts in temperate trees

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High temperature, vapor pressure deficit (VPD), and drought stress significantly alter plant hydraulics and physiology, with important consequences for the global carbon and water cycle. Yet, few studies have attempted to tease apart their effects on tree hydraulics, and address the underlying physiological drivers during hotter droughts. We experimentally assessed the single and combined effects of heat (+5°C) and drought (-50% irrigation) on leaf hydraulic traits (stomatal conductance, minimum conductance, leaf wilting tolerance, leaf water potential, and stomatal anatomy) of two contrasting temperate tree species: common beech (*Fagus sylvatica* L.) and pubescent oak (*Quercus pubescens* Willd.). Measurements were conducted for three years on young seedlings in open-top chambers. We found that while drought stress decreased stomatal conductance and shifted leaf hydraulic trait trade-offs, high temperature acting alone had little impact on leaf hydraulics. Additionally, we observed that the combination of high temperature and drought exacerbated the drought effect alone for both species.

Key message: Drought is a more decisive driver of leaf hydraulic traits for temperate trees than temperature.

Session 4-O8 - Peripheral hydraulics

Root shrinkage and recovery during edaphic drought: insights from high-resolution synchrotron X-ray CT images

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Deciphering the precise belowground processes that limit plant water uptake during drought remains a major challenge to comprehending plant drought and recovery responses. Interactive events occurring between soil and roots during soil drying appear to play a highly important role in constraining plant water use and affecting the recovery of plant functionalities under dynamic drought conditions. Belowground events can be characterized at the root level with extraordinary detail using high-resolution synchrotron X-ray microcomputed tomography (CT) images. Root shrinkage, hydraulic failure of fine root cortical cells or fine root embolism, root hair damage, or suberin deposition at exo- and endodermis cells of roots are among the most important events occurring during soil drying. However, the visualization of the interactions of roots with the soil and the rhizosphere, i.e. the soil-root interface, during soil drying and recovery after rewatering has not been sufficiently represented in the literature yet. We consider the characterization of these anatomical changes that modify soil-root interactions a fundamental first step to understanding the impact of belowground processes on both the decrease of water uptake by the roots during drought and the recovery of this function after rewatering. Thus, we conducted a specific experiment visualizing belowground processes with micro-CT in maize plants during soil drying and rewetting. This provided new insights on drought-induced root and root hair shrinkage, cortical lacunae, and air gap formation between roots and soil particles, and on how these events were reversible after recovery.



Session 4-O9 - Peripheral hydraulics

The potential role of root pressure on resistance to drought in tomato

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Water moves mainly in the xylem thanks to a gradient in negative pressure. Tomato is one of those species where xylem sap can also flow via positive pressure generated in the roots. Although this phenomenon has already been observed in several species, its physiological role has never been clarified, leaving the question why plants would invest energy during this process. We hypothesize that the generation of root pressure could help tomato plants to rehydrate its organs after drought, and possibly also repairing gas embolism in the xylem. We therefore first measured the dynamics of stomatal conductance and xylem embolism in three tomato accessions that differ in drought tolerance in leaves and stems (via optical technique, OV) and found transpiration driving the difference in drought tolerance across the accessions. Subsequently, we re-watered plants that reached different levels of stem water potential induced by drought stress, and measured the amount of root pressure. We used OV and X-ray microCT imaging to detect tissue re-hydration (leaves and stems) and possible embolism repair in xylem vessels by observing the plants before and after drought, and at different times after re-watering. Our preliminary results show that tomatoes can generate root pressures up to 40 bars, rehydrating leaves and stems even when P_{50} and P_{88} are reached. These results open new perspectives on the role of root pressure in the response of tomato to drought.

Key message: The generation of root pressure after a severe drought event could help tomato survive drought



Session 5-O0 - Concepts and methods

The functional significance of porous media and polar lipids for fluid transport in angiosperm xylem

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A longstanding question in botany is how plants are able to transport xylem sap under negative pressure without continuously developing large gas bubbles that reduce sap flow. I will address this issue by discussing the functional, mechanistic importance of the following findings: (1) dynamic changes in gas oversolubility of xylem sap, (2) the occurrence of insoluble, amphiphilic lipids with a potent surface activity in sap, and (3) the three-dimensional ultrastructure of interconduit pit membranes. The ca. 200 to 1,000 nm thick pit membranes between xylem conduits are hypothesised to produce surfactant coated nanobubbles by a local, dynamic surface tension of lipids at gas-liquid interfaces. An overview of experimental evidence on xylem transport will be presented with porous cell wall models, temporal gas dynamics, and simulations of multiphase interactions between gas, surfactants, water, and solid substances. These efforts contribute not only to our understanding of the mechanisms behind xylem sap transport, but also enable us to develop evaporation-driven transport devices without fossil fuels. Moreover, understanding hydraulic failure in plants has implications for global water conservation, plant-climate interactions, and how plants will deal with increased levels of drought at many places worldwide.



Session 5-O1 - Concepts and methods

Catastrophic hydraulic failure and tipping points in plants

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Water inside plants forms a continuous chain from water in soils to the water evaporating from leaf surfaces. Failures in this chain result in reduced transpiration and photosynthesis and are caused by soil drying and/or cavitation-induced xylem embolism. Xylem embolism and plant hydraulic failure share several analogies to “catastrophe theory” in dynamical systems. These catastrophes are often represented in the physiological and ecological literature as tipping points when control variables exogenous (e.g., soil water potential) or endogenous (e.g., leaf water potential) to the plant are allowed to vary on time scales much longer than time scales associated with cavitation events. Here, plant hydraulics viewed from the perspective of catastrophes at multiple spatial scales is considered with attention to bubble expansion within a xylem conduit, organ-scale vulnerability to embolism, and whole-plant biomass as a proxy for transpiration and hydraulic function. The hydraulic safety-efficiency tradeoff, hydraulic segmentation and maximum plant transpiration are examined using this framework. Underlying mechanisms for hydraulic failure at fine scales such as pit membranes and cell-wall mechanics, intermediate scales such as xylem network properties and at larger scales such as soil-tree hydraulic pathways are discussed. Understudied areas in plant hydraulics are also flagged where progress is urgently needed.

Keywords: bifurcation, cavitation, cusp, embolism, fold, r-shaped curves, s-shaped curves, soil, transpiration, water potential, xylem



Session 5-O2 - Concepts and methods

Dissolved gas in xylem sap is affected by water potential and temperature, but does not follow Henry's law for bulk solutions

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The concentration of dissolved gas in xylem sap is traditionally assumed to be under equilibrium following Henry's law for bulk solutions, while values above this saturation threshold are assumed to cause hydraulic failure. Yet, direct measurements of dissolved gas in xylem sap are limited to few species only. Here, the concentration of soluble gas in xylem sap was estimated *in vivo* using well-watered *Citrus* plants under varying air temperature and light, and compared to modelled data. The concentration of dissolved gas showed a daily pattern, with possible oversolubility during periods of transpiration and sap flow. Such high concentration was strongly associated with decreasing xylem water potential, and the concentration of non-dissolved gas that was present in intercellular spaces of the wood. Saturation or undersaturation of dissolved gas, however, occurred when photosynthesis was lacking. Our findings indicate that *Citrus* plants can safely transport sap oversaturated with dissolved gas, and that gas solubility does not follow Henry's law for bulk solutions. Gas oversolubility of sap could be explained by nanoconfined liquids inside cell walls. We speculate that oversolubility provides plants with a buffering capacity to avoid embolism formation by local changes in pressure and temperature.



Session 5-O3 - Concepts and methods

Define the water-use strategy: A case-study on hydraulic mechanisms regulating water use of European tree species during drought

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Continuous and long-term monitoring of water use are required to reduce uncertainties in modelling forest transpiration. Since drought threatens the vitality and survival of forests worldwide, understanding and modelling responses to drought are of particular interest. Tree species undergo strong selective pressure to develop specialized mechanisms for regulating water-use dynamics during unfavourable climatic conditions. To cope with drought a tree can adjust its “water-use strategy”, by 1) altering the regulation of water release through the leaves to the atmosphere, 2) adjusting the water storage capacitances, or 3) changing the hydraulic conductivity of the xylem. There is thus a pressing need to understand the variability of such hydraulic mechanisms and quantify how they impact forest transpiration.

Focussing on common European tree species, we present initial results from a Swiss temperate forest, where combining sap flow, dendrometer measurements and wood anatomy allowed us to disentangle species-specific differences in water-use strategies. Building upon these observations, we were able to identify species dependent trait syndromes. Moreover, a mechanistic water transport model was used to assess stem water content, stem water potential (an indicator for hydraulic vulnerability), and subsequently turgidity within the cambium (crucial for wood formation) during the summer drought of 2015. Our efforts will advance process-based understanding of drought impacts on water use and could constrain predictions of forest transpiration under changing climatic conditions.



Session 5-O4 - Concepts and methods

Xylem hydraulic conductivity measurements during flow-controlled experiments suggest the presence of gas bubbles that move with the flow and accumulate at vessel ends

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Commonly, xylem hydraulic conductance is measured by applying an above atmospheric pressure to push water through a twig. To measure twig samples at closer to natural conditions, we developed a method that applies a controlled flow rate using suction, similar to transpiration-driven flow in plants.

The setup consists of a syringe pump to control water flow, where a twig is inserted in the flow path. Hydraulic conductivity is calculated from measurements using pressure sensors and a flow meter. The syringe pump is used to generate controlled flow rates through the twig while pushing or pulling. Thus, we are able to compare our suction method with the more conventional pushing method and assess the effect of flow direction on hydraulic conductance measurements. We found a reproducible pattern in measured xylem conductivity values, where measurements using suction resulted in a 50% lower conductivity than when flow was induced by pushing. **Repeated reversals of flow revealed an intricate pattern of loss and partial recovery of conductivity, implicating the existence of particles that move with the flow and accumulate at the vessel ends.**

Here we present the intriguing results and propose an explanation capable of explaining the reproducible patterns in observed conductivity dynamics during the experiments. The explanation involves gas bubbles that shrink and swell depending on the liquid pressure, move with the flow and reduce conductivity as they accumulate at vessel ends within the xylem.



Session 6-O0 - Drought-induced tree mortality

Disentangling the impacts of atmospheric and soil droughts on forests

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Recent decades have been characterized by increasing temperatures worldwide, resulting in an exponential climb in vapor pressure deficit (VPD). VPD has been identified as an increasingly important driver of plant functioning in terrestrial biomes and has been established as a significant contributor to recent drought-induced plant mortality independent of other drivers associated with climate change. Despite this, few studies have isolated the physiological response of plant functioning to high VPD, heat, and soil drought, thus limiting our understanding and ability to predict future impacts on terrestrial ecosystems. In this presentation, I will discuss recent findings suggesting that high VPD and temperature can lead to a cascade of impacts, including reduced photosynthesis and growth as well as higher risks of hydraulic failure, independently of soil moisture changes. I will further show how compensation mechanisms associated with shifts in phenology and species interactions may mitigate the negative impacts of combined atmospheric and soil droughts.



Session 6-O2 - Drought-induced tree mortality

If a cavitation event occurred in the forest and no one was around to measure it: the role of embolism in the survival and recovery of Aleppo pine from drought

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Xylem embolism impairs hydraulic conductivity in trees and drives drought-induced mortality, yet evidence of its occurrence in mature, field-grown trees are not robust.

Seasonal patterns of embolism were monitored in Aleppo pine (*Pinus halepensis*) trees growing in a dry Mediterranean forest using Optical visualization sensors (OV) and μ CT. In addition, potted Aleppo pine trees were dehydrated in the greenhouse in order to examine the effect of embolism on their survival and recovery from drought.

In forest-grown trees, embolism increased from zero to ~12% along the dry season, with 77% of cavitation events occurring between 10:00 and 16:00. The probability for cavitation increased as vapor pressure deficit (VPD) increased, up to 42% chances for cavitation when $VPD > 5$ kPa. In potted pines, no trees with embolism levels lower than 60% had died, but stomatal conductance (g_s) following one month of rehydration was lower in dehydrated trees, proportionally to the level of hydraulic damage.

The large difference between native embolism in forest-grown pines and mortality threshold in potted ones, suggests the mature trees are not approaching hydraulic failure. However, the impaired recovery of g_s implies towards potential long-term effect of embolism on productivity, and the increased probability for cavitation with increase in VPD may encompass fatal consequences for these trees under future climate change.



Session 6-O3 - Drought-induced tree mortality

Dying of thirst: when hydraulic failure leads to cell death

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Global climatic models predict an increment in the frequency and intensity of drought events which have already shown to have important consequences on tree survival and thus forest dieback. Xylem hydraulic failure has been identified as a ubiquitous factor in triggering drought-induced tree mortality through the damages induced by the progressive dehydration of the plant living cells and thus tissues and organs. However, fundamental evidence of the mechanistic link connecting xylem hydraulic failure to cell death have not been identified yet. Working at the leaf level on three species, *Populus tremula x alba*, *Eucalyptus viminalis* and *Laurus nobilis*, the main aim of this study was to evaluate the relationship between loss of hydraulic functioning due to cavitation and cell death under drought conditions and how this relationship varied across species showing various resistance to cavitation. Thus, individuals from each species were exposed to severe drought conditions by withholding water, their vulnerability curves to cavitation at the leaf level constructed, and their leaves sampled to measure their relative water content (RWC_{Leaf}) and electrolytes leakage (EL). Results showed that cavitation always precedes cell mortality at the leaf level for the three species. They also evinced a critical RWC value (RWC_{crit}) for cellular integrity that varies with the species resistance to cavitation.

Session 6-O4 - Drought-induced tree mortality

Mechanisms underlying holm oak recovery after water stress: is the carbon reserves consumption unavoidable to maintain xylem hydraulic functionality?

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Quercus ilex dieback was observed in Mediterranean forests after drought events. We investigated the physiological and molecular mechanisms linked to embolism formation and depletion of carbon reserves in *Q. ilex* seedlings exposed to severe water stress and rewatering. Coordinated measurements of gas exchange, water relations, non-structural carbohydrates, drought-related genes expression and anatomical changes in wood parenchyma were assessed. Under water stress, stem midday water potential of - 4.6 MPa, corresponding to ~ 50% loss of hydraulic conductivity, and prolonged stomatal closure led to the depletion of carbon reserves. Carbohydrates consumption, resulting by the upregulation of a β -amylase gene (*BAM3*) and the downregulation of glucose (*GPT1*) and sucrose (*SUC27*) transport genes, suggested glucose utilization to sustain cellular metabolism. After rewatering, the partial recovery of photosynthesis allowed the storage of carbohydrates in the wood parenchyma and the formation of new vessels. Changes in cell wall composition of fibers were also observed, probably helping regulate water storage in stem tissues. Our results show that, under severe water stress, *Q. ilex* preserve xylem functionality at the expense of wood carbon reserves. This may expose this species to the risk of carbon starvation, compromising its survival in Mediterranean environments exposed to recurrent drought spells.



Session 6-O5 - Drought-induced tree mortality

Mutually inclusive mechanisms of drought-induced tree mortality

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The unprecedented tree dieback caused by the 2018 summer drought in Central Europe highlights the need for a better mechanistic understanding of drought-induced tree mortality. While previous research has singled out numerous risk factors, the principal mechanisms are still debated.

We studied 9435 young trees of 12 temperate species to assess how hydraulic traits, carbon dynamics, pest infestation, tree height and neighborhood competition influence individual mortality risk in the 2018 drought, which resulted in the loss of a third of the trees.

Species with narrower hydraulic safety margins and an increasing sugar fraction in their non-structural carbohydrate pool were more likely to die. Individual risk was higher for trees affected by bark beetles, smaller trees, and trees that received less shelter from their neighbors, though neighborhood interactions were strongly species-specific.

Our data show that while severe tissue dehydration driven by hydraulic failure marks the final stage of drought-induced tree mortality, it interacts with other, mutually inclusive processes. These include starch depletion for osmotic adjustment and pest infestation, and are modulated by size effects and neighborhood interactions. A more holistic view that accounts for multiple causes of drought-induced tree mortality is required to improve predictions of trends in global forest dynamics.



Session 6-O6 - Drought-induced tree mortality

Hydraulic safety margins in South African plant communities: how close are they to the edge?

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Embolism in the plant xylem transport network is a disruptive process leading to loss of function and damage in downstream tissues. Plant susceptibility to loss of function can be assessed at any time point by coupling knowledge of static xylem physical tolerance limits with dynamic xylem pressure potential. Here, we examine the embolism avoidance hypothesis in diverse South African biomes, testing the central claim that these plants tend to avoid any loss in hydraulic conductivity under normal conditions, only exceeding critical water potentials under severe water stress. We quantified the water potential difference between the minimum seasonal water potential (P_{\min}) and the water potential associated with 50% loss of hydraulic conductivity (P_{50}), typically referred to as the hydraulic safety margin ($\text{HSM}_{P_{50}}$). Xylem susceptibility to embolism (P_{50}) was quantified using the optical technique. P_{\min} was assessed using water potential data from two sites over two rainfall years. Our results show that only one out of twenty two species surpassed the P_{50} threshold in the drier year, and that only two species displayed any embolism at all at the drier study site. Functional types converged in HSM, despite varying physical tolerance limits. The majority of species (> 80%) maintained HSM greater than 1 MPa, which differs from reports that globally 70% of all angiosperm species operate at narrow (< 1 MPa) HSM. We propose that conservative safety margins may have evolved in response to nutrient impoverishment of the underlying substrate, to maintain leaf function for multiple years.



Session 6-O7 - Drought-induced tree mortality

Mixing isohydric and anisohydric tree species increases water use but improves hydraulic safety margins during extreme drought

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Tree diversity is regarded as a mean to adapt forests to climate change and build successful reforestation programs. Current data indicate that species mixtures with distinct drought response strategies can increase the drought resistance of tree plantations, but the underlying mechanisms are not clear. In this study, we aimed to assess whether mixing iso- and aniso-hydric species dampen water stress compared to monoculture. We setup a greenhouse experiment to monitor the physiological responses to drought of *Pinus halepensis* (drought avoider or isohydric) and *Quercus ilex* (drought tolerant or anisohydric) seedlings planted in pots, in monoculture or in mixture. We monitored soil water content, gas exchanges and water potentials for each composition. We show that the soil water potential was lower in the mixtures indicating a greater water use. However, under mixture conditions, the predawn water potential and the safety margins of *Q. ilex* were higher (improved), while the safety margins of *P. halepensis* remained unchanged. By using the plant hydraulic SurEau model, we show that this species-specific diversity effect is related to different traits combinations including changes in stomatal regulation and rhizosphere conductance. These results have important implication to understand how biodiversity modify trees and forest drought resilience.

When the heat was on: long-term limitations of xylem hydraulics after forest fires

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Forest fires of low and moderate intensity often do not constitute a direct lethal threat to mature trees, but rather, leave behind trees with a variety of injuries, subsequently affecting their physiology. Post-fire physiological processes and linking specific heat injuries to impairments of whole-tree functioning are the focus of current research. Recent studies suggest that, besides cambium and phloem necrosis, fire-induced xylem dysfunction plays an important role in post-fire tree physiology.

We analyzed how heat transferred to the xylem can alter conduit structures in branches, consequently limiting stem hydraulic conductivity as well as hydraulic safety after fires. Post-fire xylem dysfunctions in mature tree trunks were monitored in situ via electrical resistivity tomography, and measurements of trunk diameter variations and basal area increments of injured trees allowed to link heat-initiated hydraulic limitations with tree functionality and growth in the years after fire. Finally, we integrated potential hydraulic dysfunctions into a conceptual framework, which explains post-fire physiological processes, their interactions and possible feedbacks.

Considering climate-driven changes in fire activity, knowledge on post-fire tree responses will become increasingly important to better estimate respective forest ecosystem dynamics and interactions with other disturbances such as drought events or biotic attacks.



Session 7-O0 - Xylem structure and function

Save it for a rainy day? Evaluating dynamic changes in conduit functional status relative to water storage of neighboring cells across several woody plant species

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Xylem tissue is comprised of various cell types with divergent function. Conduits are responsible for water transport, and are surrounded by a matrix cells that function in storage, metabolism, or structural support. These various cells, with varied arrangements across organs, are thought to impact the functional status of conduits. Recent studies utilized X-ray microCT to observe changes in the water status of secondary xylem matrix for a couple of woody species. They found that fibers emptied after xylem embolism, suggesting a limited role in buffering tensions during drought. Since it is unknown whether this pattern is widespread across species, we evaluated stem water storage for several North American tree species. We observed two dominant patterns; in the first, the xylem matrix was primarily air-filled all the time, while in the second group the matrix remained water-filled until severe drought. None of the species appear to use stored capillary water to minimize the risk of embolism, and the matrix did not readily refill. In a parallel study, we evaluated the role of living parenchyma cells in water storage dynamics of leaf petioles, and found varying patterns involving pith water depletion that preceded cell collapse and distortion at the whole organ level that impacted hydraulic function. Results from both studies will be related to specific xylem anatomical features and cell organization across the species and organs.



Session 7-O1 - Xylem structure and function

Hydraulic strategies associated with water storage in woody plants across water availability gradient

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Water storage in plants is an important player in plant water balance and dynamics. It could help meet plant water demands (especially during hot/dry weather) and buffer the effect of sudden changes in environmental conditions. This could also underpin how hydraulic traits are coordinated in plants across habitats with different water availability. We used sapwood capacitance (C_s) as a measure of plant's internal water storage capacity as it is the amount of stored water released per unit sapwood volume for a unit change in xylem water potential. We compiled a dataset including C_s and 7 hydraulic traits for 149 species across 16 sites around the globe to explore (1) how C_s influences the xylem safety (P_{50}) - efficiency (K_s) tradeoff across species and (2) how hydraulic traits coordinate with C_s and aridity index.

Main message: We found that C_s could represent an important drought-avoidance strategy. Tall species with high leaf-to-sapwood area ratio, low sapwood density, high K_s , less-negative P_{50} and less-negative stem water potentials at predawn and midday generally have high C_s values. This could represent a single axis of coordinated plant hydraulic strategies along a water availability gradient with important implications for plant responses to emerging climatic changes.



Session 7-O2 - Xylem structure and function

Distinguishing genetic, ontogenetic and spurious xylem adaptations to aridity

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Xylem anatomy is responsible for the efficient and safe water transport in plants. However, interpreting the variation of xylem traits as adaptations to water deficit is fraught with issues that can bias comparisons or lead to unjustified conclusions. Using different datasets of intra- and interspecific variation in wood anatomy, I look for evidence of various xylem traits being adaptive to aridity, highlight potential pitfalls and biases and try to distinguish ontogenetic from phylogenetic variation. Species compositions and intra-specific variation change along gradients of water deficit for reasons unrelated with xylem adaptations, which requires a careful selection of species or provenances to compare. Many wood traits change with tree size (some for hydraulic reasons) and particularly in ring-porous species with the early/latewood ratio, so tree size and growth rates need to be accounted for. Using a dataset of 466 tree species and accounting for tree size and the relatedness of species showed that **while most wood traits tested do respond to aridity, genetic and/or phenotypic adaptations on average explained only 3% of trait variation while tree size explained 8% and phylogeny 50%.** Overall, I found more evidence of phenotypic compared to genetic adjustment to water supply. While both reflect adaptations in xylem structure, the interpretation of genetic vs. phenotypic adjustment differs substantially.



Session 7-O3 - Xylem structure and function

Xylem functional trait trade-offs and tree species responses to drought and cold stresses in NA and EU forests

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Trees allocate resources to optimize growth and survival, resulting in broad trade-offs between functional traits. Tree responses to stresses (e.g. frost and drought) and inter-specific interactions (e.g. competition) drive forest demographics and species range evolution. Under climate change, understanding these dynamics is critical, as climate extremes will likely become more common in many regions, with already visible potential impacts such as widespread mortality events.

We investigated trade-offs between xylem functional traits linked to survival (drought and frost resistance) and resource acquisition and competition traits (DBH, wood density, tree height), and how these interactions shape tree species distributions across North-American and European forests. We used existing and novel trait measurements to build a database with over 1000 tree species to assess xylem functional trait relationships, and combined this with growth and demographic data from forest inventories from several NA and EU countries. We find that coordination between resistance traits limits the ability of species to be competitive, driving both species distributions, and explaining the common occurrence of species with low resistance in mild habitats (neither too dry nor too cold). This leaves these so-called incompetent species vulnerable to dramatic changes in climate.

Key message: Key xylem functional trait trade-offs around drought / frost tolerance and competition determine forest species vulnerability to climate change across North-America and Europe

Session 7-O4 - Xylem structure and function

Maintaining leaf hydraulic conductance constant for constant carbon cost: the interplay of xylem traits

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Across species, water-transporting conduits in the xylem of trees widen in similar ways from the stem tip toward the base. This tip-to-base conduit widening offsets the increase in hydraulic resistance due to increasing path length, maintaining leaf hydraulic conductance \sim constant as a tree grows taller. However, this scenario would seem necessarily to force plants to invest progressively more sapwood carbon per unit leaf area because conduits become progressively longer. However, empirical evidence in shows that in angiosperms conduits at the stem tips are wider in taller trees, suggesting a possible interplay of anatomical traits that might minimize both hydraulic resistance and the cost of carbon for supplying progressively more distant leaves. Conduits that are wider at the tip are, for the same tip-to-base widening rate, wider along the entire pathlength and so have lower resistance. Lower per-conduit resistance means that taller plants, with their wider terminal twig conduits, can potentially supply the same leaf area with fewer, though wider, conduits. Fewer conduits for the same leaf area is a potential mechanism by which trees maintain living sapwood carbon costs constant per unit leaf area as they grow taller; selection should always favor individuals with the lowest possible increase in metabolically active sapwood per unit leaf area with height growth. We propose how this interplay might manifest in conifers, which generally have conduits that remain relatively constant in diameter at the stem tip with height growth.



Session 7-O5 - Xylem structure and function

Two path length effects emerging from ontogenetically stable axial xylem design affect the conductance of inner sapwood rings

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The process of sapwood/heartwood transition in trees is not fully understood. We tested whether the ontogenetically-stable apex-to-base conduit widening generates path length effects limiting the conductance of inner sapwood rings.

The axial scaling (b) of conduit hydraulic diameter (D_h) was estimated at annual resolution in a spruce and beech tree. We compiled a global dataset of sapwood ring number ($NSWr$), their average width ($SWrw$), tree height (H) and stem elongation rate (ΔH) in conifer and angiosperm trees. A numerical model simulated the effects of H and ΔH on the conductance of each xylem ring (K_{RING}).

b resulted ontogenetically stable. Simulations well predicted the observed patterns of increasing $NSWr$ with H and decreasing $NSWr$ with ΔH , assuming that heartwood forms when the marginal conductance gain of maintaining the functionality of an inner ring becomes negligible.

Sapwood/heartwood transition minimizes the C costs associated to allocation to secondary growth and maintenance of living sapwood required to attain a given sapwood conductance. **The number of sapwood rings depends on the effects of H and ΔH on the conductance of inner sapwood rings. The width of sapwood rings contributes to compensate for the lower conductance of inner sapwood rings at high ΔH .**



Session 8-O1 - Ecosystem water fluxes

²H₂O Pulse-Labeling traces the role of different hydraulic strategies, utilization of deep water reserves and water transport times on ecosystem drought response and recovery

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Severe droughts are increasing worldwide, however, how different hydraulic adaptations drive ecosystem water during drought and recovery remains poorly understood. To disentangle complex ecosystem dynamics we imposed a 9.5-week drought on the Biosphere 2 tropical rainforest in the Water, Atmosphere, and Life Dynamics (B2WALD) experiment [1]. We continuously measured atmospheric conditions, soil water content and tree sap flow, stem water content. We used novel in situ approaches to monitor the isotopic composition in soils, tree xylem and transpiration at high temporal resolution. A ²H-labelled deep-water label during severe drought provided a unique opportunity to evaluate transit times and legacy effects during the recovery phase. Drought-sensitive canopy trees strongly reduced water fluxes during early drought, while drought-tolerant trees increased their relative contribution to total water flux. Interestingly, all deep-rooted canopy trees tapped into deep-water reserves, but spared deep water reserves until severe drought and exhibited long transit times of 2-6 weeks until d²H-labelled water was transpired. This was partially due to stem water refill exceeding the onset of transpiration after drought release.

These data highlight the importance of quantifying drought impacts on forest functioning beyond the intensity of (meteorological) drought, but also taking dynamics response of hydraulic regulation of different vegetation compounds and soil microbial activity of the forest into account.

[1] Werner et al. 2021 Science 374, 1514 DOI: [10.1126/science.abj6789](https://doi.org/10.1126/science.abj6789)

Bedrock as a water source for trees under drought: experimental evidence and model simulations

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Large portions of the terrestrial habitats are characterized by shallow (< 50 cm) soils overlying more or less compact bedrock and the contribution of water stored in rock pores to the total water storage can be substantial. It is not clear to which extent this water can be exploited by plants under drought, and this might depend on rock characteristics such as porosity, pore connectivity and hydraulic conductivity, but also on root hydraulics and rock-root connection.

Fraxinus ornus trees growing in Classical Karst on two different bedrock formations, i.e. in breccia (more porous, higher plant available water content, AWC) and dolostone (less porous, lower AWC), maintained under summer drought a better water status in the former than in the latter population. Subsequently, a more detailed study on hydraulic conductivities of the single components of the system, i.e. rocks (breccia and dolostone), soil, roots and whole plant was performed in controlled potted systems, with *F. ornus* saplings grown in soil-rock mixtures and subjected to well-watered and drought conditions. Finally, based on the collected empirical data, 2D model simulations of the rock-to-root water exchange have been run. Such simulations suggested higher exploitation of water pools in the breccia than in the dolostone systems in the dry range (soil water potentials between -1.0 and -1.5 MPa). These results support the field evidences and suggest considering bedrock available water for a better comprehension of spatial variations in vegetation water status and dieback patterns in rock-dominated landscapes.

Session 8-O3 - Ecosystem water fluxes

Tree water use resilience from sap flow data: towards a characterisation of tree drought responses in their temporal context

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Our global understanding of tree physiological responses to drought is mostly based on static traits and tree water use or status regulation in response to hydrometeorological variability. However, these approaches overlook drought recovery processes and miss many aspects related to the temporal dimension of drought responses. Drought resilience studies based on global and regional assessments of tree radial growth, ecosystem fluxes, and remotely-sensed vegetation properties have shown an enormous diversity of recovery patterns, across different environments. Here, we propose a roadmap to quantify water use resilience from tree-level sap flow time series to better understand the ecophysiological underpinnings of these patterns. Using some example datasets from the SAPFLUXNET database, we will (i) show how to identify and characterise individual drought events, (ii) propose a set of resilience metrics applied to sap flow and/or canopy conductance, (iii) discuss how tree water use resilience can provide insights on the mechanisms underlying dynamic drought responses (i.e. changes in hydraulic conductance) and (iv) devise how this knowledge can help improve terrestrial ecosystem models.

Key message: An analysis of the global spatiotemporal patterns of water use resilience from sap flow can greatly improve our understanding of the dynamic nature of drought responses in their temporal context.



Session 8-O4 - Ecosystem water fluxes

Height-related sap-flow responses to VPD: a global-scale analysis of tree function under drought

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The predicted increase in temperatures with climate change will force elevated atmospheric vapour pressure deficit (VPD), which induces higher leaf transpiration rates and/or stomatal closure. This can have strong implications for ecosystem water and carbon cycles and their feedbacks with climate. Tree size may alter the timing and strength of tree responses to water deficits, with taller trees being theoretically more vulnerable to drought and increasing VPD than shorter, understory trees because of their intrinsically stronger hydraulic constraints associated to their longer hydraulic pathway and higher exposure to solar radiation and VPD. We assessed how height affects tree response to VPD within and across species through its effect on sap flow and, thus, on tree transpiration and canopy conductance to water vapour, using the global database SAPFLUXNET. We used data from 76 species from 110 sites. The mean height of the trees evaluated was 17 ± 9 m, with an average intra-specific within-site range of 9 ± 8 m. Whole-tree sap flow significantly increased with height, both within and across species.

Key message: Taller trees started transpiring earlier in the day than shorter conspecifics, with sap flow diel dynamics being more decoupled from those of VPD in the former, indicating a heavier use of xylem water reserves in taller than shorter trees.



Poster presentations

Session 2-P1 - Variability in plant hydraulic traits

Far from constant: Hydraulic traits in first year tree seedlings

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Fundamental structural changes during seedling establishment require constant physiological modifications to enable well-balanced water relations and optimized carbon uptake. Hydraulic studies on seedlings though are rare, as most classical methods cannot be applied on tiny plantlets. In this study, changes in cell osmotic parameters, shoot hydraulic conductance and cavitation resistance were evaluated on six Alpine woody species during their establishment from three to 29 weeks old plants.

Hydraulic parameters were obtained with psychrometric water potential measurements, the pressure-volume technique, the evaporative flux method and ultrasonic emission analyses, and outcomes related to various leaf and xylem anatomical parameters (leaf and xylem area, conduit diameter, cell wall reinforcement).

In all species, shoot hydraulic conductance was highest in youngest stages, indicating an exceptionally good water supply of newly germinated seedlings. Around week 10, it leveled off at lower but, due to well-balanced xylem and leaf anatomical modifications, stable values until the end of the first growing season. In contrast, turgor loss point, osmotic potential at full saturation and cavitation resistance pointed to a continuous increase in drought tolerance. Outcomes reveal well-coordinated structural and physiological changes to allow for stable water relations.

Key message: Hydraulic and related structural traits are constantly adjusted across the first growing season, whereby the first weeks are characterized by high water supply to compensate for low drought resistance.



Session 2-P2 - Variability in plant hydraulic traits

Assessing tree diversity effect on tree resistance to drought through hydraulic safety margins

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Forest ecosystems are suffering more frequent and intense drought that is threatening tree survival and forest functions. Tree diversity is generally regarded as a mean to increase resistance to drought, but we lack explanatory mechanisms, which limits our ability to design relevant species mixtures in restoration and afforestation programs. Plant hydraulic framework can be used to understand if and how tree diversity can improve the resistance of trees to drought. Here, I present the first chapter of my PhD project, in which I quantify the potential changes in resistance to drought of various tree species planted along diversity gradients (from monoculture to 5 species mixture). Measurements have been done during summer 2021 and 2022 in five experiments planted as part of the Treedivnet network and located in five different European countries. To this end, I quantified the hydraulic safety margin, defined as the difference between exposure to stress (the plant water or osmotic potential during summer drought) and the vulnerability to stress (estimated as the water potential causing 50% xylem embolism) along the different diversity gradient. The results will help to quantify whether drought resistance changes with diversity and if those changes are related to exposure or vulnerability.

Session 2-P3 - Variability in plant hydraulic traits

Differences in seasonal sensitivity of xylem hydraulic conductivity to ions in sap between ring- and diffuse-porous tree species

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Ion-mediated changes in hydraulic conductivity (ΔK_h) represent a mechanism allowing plants to regulate the rate of xylem transport. However, the significance of ΔK_h for ring-porous (RPS) and diffuse-porous tree species (DPS) remains unknown. We examined ΔK_h in juvenile branches of three coexisting, temperate RPS (*Fraxinus excelsior*, *Quercus robur*, *Robinia pseudoacacia*) and three DPS (*Acer pseudoplatanus*, *Carpinus betulus*, *Fagus sylvatica*) across the whole year, and assessed the relationships of ΔK_h to branch anatomy. RPS exhibited twice as higher ΔK_h (10.3% vs 5.3%) within the growing season (i.e., during wood production) compared with DPS, and the production of the annual ring was identified as a crucial process affecting maximum ΔK_h within the season. In addition, xylem in branches of RPS generally contained more axial parenchyma (AP; 18% vs 7%) and was characterized by a greater relative contact fraction between vessels and parenchyma (F_{VP} ; 59% vs 18%) than xylem in DPS. Simultaneously, ΔK_h measured within the growing season was positively correlated with AP, F_{VP} , and bark proportions, suggesting that parenchyma in branches may be important for high ΔK_h . A significant increase in ΔK_h observed during the growing season may help RPS to restore conductive capacity after winter, better compensate for transport loss by drought-induced embolism, and thereby improve water delivery to leaves.



Session 2-P4 - Variability in plant hydraulic traits

A trait-based assessment of drought resistance among 21 commercial *Eucalyptus* genotypes in Brazil

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The increased intensity and frequency of drought caused by ongoing climate change is affecting forest worldwide. *Eucalyptus*, the most widely planted genus in tropical regions, already suffered from large-scale drought-induced mortality events, urging for the search of more resistant species or varieties. Here, we use a field common garden located in southern Brazil to evaluate how drought responses vary among 21 commercial *Eucalyptus* genotypes. Leaf turgor loss point, g_{min} , deciduousness (LAI changes between dry and rainy season), height, predawn and midday leaf potential, root front depth and xylem vulnerability to cavitation are compared among genotypes. We also explore whether there is a trade-off between drought resistance and stand above-ground productivity among *Eucalyptus* genotypes. Our study has important implication for the management and sustainability of tropical *Eucalyptus* plantations under climate change.



Session 2-P6 - Variability in plant hydraulic traits

High variation in branch-tip xylem vulnerability decreases basipetally down the stem in *Callitris rhomboidea*: insights into strategies for drought survival and future measurements of xylem vulnerability

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Continuous monitoring of xylem embolism across whole plants allows us to investigate the propagation of drought-induced xylem damage *in vivo*. Information on embolism propagation and intra-plant variation in xylem vulnerability has major implications for how we quantify both species, and individual-level xylem vulnerability. Optical monitoring of drought-induced xylem embolism throughout the canopy of a drought-resistant conifer, *Callitris rhomboidea*, revealed wide variation in xylem vulnerability among small branchlets. Optical vulnerability measurements in branches with varying diameters showed that variation in xylem vulnerability is greatest at these small diameter branch-tips in this species, with P_{50} s found to become more consistent moving basipetally down the stem. This information contributes to our understanding of how drought-resistant trees like *C. rhomboidea* survive drought, and provides evidence to inform future measurements and interpretation of xylem vulnerability data.



Session 2-P7 - Variability in plant hydraulic traits

Xylem anatomy explains intraspecific variability of Ψ_{50} and $d^{13}C$ in European beech provenances

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European beech provenances show great phenotypic plasticity in anatomical, morpho-physiological and dendrometric traits. The understanding of underlying mechanisms and constraints behind phenotypic variation is necessary for proper assessment of the adaptive potential of European beech under global climate change. Xylem anatomy, vulnerability to xylem embolism and leaf carbon isotope signature of seven European beech provenances planted in two common garden sites in Germany and Slovakia were tested in this study. The results showed significant differences in provenance \times site interaction for xylem pressure at 50% loss of hydraulic conductance (Ψ_{50}) and carbon isotope signature ($d^{13}C$). Moreover, Ψ_{50} showed a positive significant relationship with theoretical specific conductivity. Thus, provenances show trade-off between xylem conductivity and xylem embolism resistance. On the other hand, the $d^{13}C$ showed a negative significant relationship with the Carlquist vulnerability index. Henceforth, provenances with the greater ratio between vessels diameter and density show greater water use efficiency derived from the $d^{13}C$.



Session 2-P8 - Variability in plant hydraulic traits

Diversity of hydraulic traits in tropical montane tree species

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Montane rainforests are biodiversity hotspots with high productivity. However, they suffer from increased mortality and declining relative abundance in a changing climate. Few studies have been conducted to explore the hydraulic traits, mechanisms and processes controlling climate-induced mortality in tropical montane trees. Using the unique TRopical Elevation gradient Experiment in Rwanda (Rwanda TREE, www.rwandatree.com), we study the diversity of hydraulic traits and water-use strategies in tropical trees and how these are linked to the variation in growth and mortality among species. Rwanda TREE consists of large multispecies plantations with 5400 trees of 20 species growing in mixed stands at three sites with different elevations (1300-2400 m above sea level) and climates (15-21 °C mean annual temperature). Water manipulation treatments are applied at each site (irrigation, rainfall exclusion). We measure hydraulic traits and processes such as leaf water potential, sap flow, whole-tree hydraulic conductance, tree water capacitance, Huber value, leaf minimum conductance, species defoliation strategy and functional rooting depth. Preliminary results on these traits and processes will be presented and related to growth and mortality data, which have been collected since the start of the study in 2018.

Key message: Using a unique field experiment in Rwanda, we study the interspecific variation and plasticity of hydraulic traits in montane tropical trees exposed to warmer and/or drier climates and how these are related to tree growth and mortality.

Session 2-P9 - Variability in plant hydraulic traits

The role of multiple hydraulic traits plasticity on hydraulic failure: an analysis based on data and model analysis

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Leaf and xylem hydraulic traits, such as leaf area, stomatal regulation of transpiration, cuticular conductance and vulnerability of the hydraulic system, determine plant desiccation dynamics during drought. However how the plasticity of these traits affect the overall leaf and plant performance under increasing drought is rarely quantified. In the present study, we used three rainfall exclusion experiments established in mature forests in Southern France - namely Font-Blanche, Puéchabon and O3HP experimental sites- to evaluate the plasticity of leaf and xylem hydraulic traits under aggravated drought conditions for the three Mediterranean species: *Quercus ilex*, *Quercus Pubescens*, and *Pinus halepensis*. For *Pinus halepensis* and *Quercus pubescens*, no significant differences were found between treatments for any traits, in accordance with field measurements of minimum water potential. By contrast, *Quercus ilex* exhibited lower turgor loss point (Ψ_{tlp}) and embolism resistance in the exclusion treatments but g_{min} remained similar. In addition changes in leaf area were recorded in the exclusion treatments for both *Quercus ilex* and *Pinus halepensis*. We then used the plant hydraulic model SurEau-Ecos to quantify the plasticity effect on whole plant transpiration and hydraulic failure for *Quercus ilex* as we found the highest degree of trait plasticity. The model allows to quantify the relative contribution of the plasticity of the different traits to hydraulic failure and cumulated transpiration under current and future conditions.

Session 2-P10 - Variability in plant hydraulic traits

Water relations of two apple cultivars under irrigation

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Because of an increased incidence of drought, irrigation has become an important agricultural practice in mesic regions that did not previously require water addition. Efficient irrigation scheduling depends on a good knowledge of tree water relations. Among other parameters, stem water potential (Ψ_s) is an essential indicator of tree water status. For three growing seasons, we monitored Ψ_s in two apple cultivars (*Malus × domestica*) with and without irrigation. We also determined P_{50} and vessel diameters in annual shoots and petioles. To evaluate if the trees are capable of osmotic adjustment, we conducted repeated measurements of turgor loss point (TLP), osmotic pressure at full turgor, and the concentrations of organic osmotic substances (proline, glucose, sucrose, sorbitol) in leaves. We found that Ψ_s did not drop below -1.6MPa during the three seasons of monitoring, which is well above the P_{50} and TLP. The triploid variety Red Jonaprince had typically lower values of Ψ_s than the diploid variety Gala Brookfield. Red Jonaprince also showed more vigorous growth and greater vessel diameters in shoots and petioles than Gala. Irrigated trees had higher Ψ_s than trees without irrigation, but the difference was rather small. Concentrations of all measured osmotics were higher in leaves of non-irrigated trees of Gala and increased during the season, while the pattern was more variable in Red Jonaprince. Taken together, our results indicate that Red Jonaprince is potentially more susceptible to drought stress than Gala Brookfield and hence has greater needs for irrigation.



Session 2-P11 - Variability in plant hydraulic traits

The lesson from two long term precipitation exclusion experiments: xylem plasticity is not a real option in trees

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Long-term throughfall precipitation exclusion experiments (TEEs) are strategic to better understand the acclimation potential of tree species to the increasing occurrence of drought conditions. We investigated xylem and phloem anatomical traits on apical branches from two throughfall precipitation exclusion experiments (TEEs). In the Sevilleta Long Term Ecological Research (LTER, New Mexico, USA) Piñon pine (*Pinus edulis* Engelm.) trees were subjected to four treatments: control (CO), 10 years of 45% rain-off (Legacy), 1 year of 45% rain-off (New45) and 90% rain-off (New90). In the “Kranzberg Roof Project” (KROOF) (Bavaria, Germany), Norway spruce (*Picea abies* Karst.) and beech (*Fagus sylvatica* L.) trees were subjected to two treatments for 5 years: control (CO) and full throughfall-exclusion during the growing season (TE).

Experimental results showed that the xylem conduits increased in diameter from the apex downwards along the main branch axis and no significant differences emerged in the drought treatments from control trees in both LTER and KROOF experiments. Only at the LTER, a marginal increase in tracheid diameter resulted significant for the New90 treatment. Phloem sieve elements resulted larger in the Legacy treatment at Sevilleta but showed no significant differences between treatments in both species at the KROOF experiment. Strong reduction in soil water availability inducing only marginal changes in the anatomy of xylem and phloem should stimulate a thorough rethinking of the concept of climate-induced phenotypic plasticity of the xylem and phloem anatomy in trees.

Integrating multiscale tree-level radial growth with satellite-derived phenology to model the productivity dynamics of European beech at its warmest distribution margin in Foresta Umbra and Sfilzi National UNESCO forest reserves

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Daily to annual stem radial increments have been recorded through an ensemble of measuring approaches in 6 heterotopic *Fagus sylvatica* L. populations spanning a steep thermal gradient covering some of the warmest conditions for the species. Electronic dendrometers, metal dendrometer bands and tree rings have been used to describe stem growth dynamics at the daily, seasonal and annual time scales 2018-2021. Land surface phenology dynamics from different satellite sources allowed to quantify intra-annual tree and forest canopy developments and photosynthetic dynamics. The interplay among climate, phenology, photosynthesis and growth was quantitatively assessed to determine how seasonal dynamics in water and heat availability interact with tree size in shaping tree productivity changes along the thermal gradient.



Session 2-P13 - Variability in plant hydraulic traits

Climate context drives hydraulic traits spatial variation across Amazon forests

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⁶TREMOR: Mechanisms and consequences of increasing TREE MORTality in Amazonian rainforests, <https://bit.ly/3BqLmuJ>

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Amazonia is the largest and most diverse tropical forest on Earth, playing a fundamental role in the global biogeochemical cycles. In the past decades, Amazon forests have faced increase in drought frequency, which resulted in elevated tree mortality, biomass loss and may have contributed the observed decline of the long-term Amazon carbon sink. Future climate conditions are predicted to intensify water stress over Amazonian forests, yet our capacity to foresee how these forests will respond to changes in climate is limited by a lack of basin-wide understanding of their inherent ability to resist water stress. Hydraulic failure, defined as the disruption of water transport within the xylem due to embolism, has been reported as the major mechanism leading to drought-induced tree mortality. The water potential at which 50% of xylem conductivity is lost (Ψ_{50}) is a frequently used metrics of embolism resistance. Besides this, it is also important to determine how close trees get to critical embolism thresholds under natural conditions, as defined by their hydraulic safety margin (HSM₅₀). Here, we present the first basin-wide tree hydraulic traits dataset, encompassing 129 tree species and spanning effectively the entire precipitation gradient of the Amazon basin. We used this dataset to assess whether there is variation in drought vulnerability within Amazonia. We find variable patterns of Ψ_{50} and HSM₅₀ within Amazonia, being both strongly related with climate context e.g. MCWD – maximum climatological water deficit), indicating different ability of these forests to cope with a future hotter and drier climate.

Session 2-P14 - Variability in plant hydraulic traits

Drought acclimation of *Quercus ilex* leaves improves tolerance to moderate drought but not resistance to severe water stress

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Increasing temperature and drought can result in leaf dehydration and defoliation even in drought-adapted tree species such as the Mediterranean evergreen *Quercus ilex* L. The stomatal regulation of leaf water potential plays a central role in avoiding this phenomenon and is constrained by a suite of leaf traits including hydraulic conductance and vulnerability, hydraulic capacitance, minimum conductance to water vapor, osmotic potential and cell wall elasticity. We investigated whether the plasticity in these traits may improve leaf tolerance to drought in two long-term rainfall exclusion experiments in Mediterranean forests. Osmotic adjustment was observed to lower the water potential at turgor loss in the rainfall-exclusion treatments, thus suggesting a stomatal closure at more negative water potentials and a more anisohydric behavior in drier conditions. Conversely, leaf hydraulic conductance and vulnerability did not exhibit any plasticity between treatments so the hydraulic safety margins were narrower in the rainfall-exclusion treatments. The sequence of leaf responses to seasonal drought and dehydration was conserved among treatments and sites but trees were more likely to suffer losses of turgor and hydraulic functioning in the rainfall-exclusion treatments. We conclude that leaf plasticity might help the trees to tolerate moderate drought but not to resist severe water stress.

Key message: Trees exposed to long-term increased drought exhibit plasticity in leaf traits that improves their functioning under moderate water stress while putting them at greater risk of hydraulic failure during severe drought.



Session 3-P1 - Plant hydraulic models

From field data experiments to land surface models: Exploiting the opportunity of xylem functional traits to drive the modelling of plant water transport

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Including plant hydraulic traits (PHTs) in land surface models (LSMs) provides the opportunity to characterize the impact of the different water-use strategies (WUS) of tree species on the simulated transpiration of forested ecosystems. However, the spatial representation of vegetation in LSMs requires homogenising the PHTs using the plant functional type (PFTs) classification system. The focus of this work is to understand the impact of the PHTs variability in the transpiration response modelled with the Community Land Model 5.0 (CLM5). We carried out multiple numerical experiments across European sites by integrating experimental evidence of different degrees of vulnerability of tree species. We show that the PFTs are poor predictors of the WUS leading to a poor predictive skill of the vulnerability to hydraulic failure. To improve the predictive capacity of LSMs such as CLM5 it is necessary to address the tree species' plasticity, improving the knowledge of how environmental conditions and ontogeny shape the maximum xylem conductance (k_{\max}) and 50% loss of conductance (Ψ_{p50}) that determines the plant water transport in CLM5. Also, we point out the need to understand how droughts and extended dry periods affect the recovery process and how the PVC changes after different degrees of water stress.

Session 4-P1 - Peripheral hydraulics

Herb and conifer roots show similar high sensitivity to water deficit

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Root systems play a major role in supplying the canopy with water, enabling photosynthesis and growth. Yet, much of the dynamic response of root hydraulics and its influence on gas exchange during soil drying and recovery remains uncertain. We examined the decline and recovery of the whole root hydraulic conductance (K_r) and canopy diffusive conductance (g_c) during exposure to moderate water stress in two species with contrasting root systems: *Tanacetum cinerariifolium* (herbaceous Asteraceae) and *Callitris rhomboidea* (woody conifer). Optical dendrometers were used to record stem water potential at high temporal resolution and enabled non-invasive measurements of K_r calculated from the rapid relaxation kinetics of water potential in hydrating roots. We observed parallel declines in K_r and g_c to <20% of unstressed levels during the early stages of water stress in both species. The recovery of K_r after rewetting differed between species. *T. cinerariifolium* recovered quickly, with 60% of K_r recovered within 2 h, while *C. rhomboidea* was much slower to return to its original K_r . Recovery of g_c followed a similar trend to K_r in both species, with *C. rhomboidea* slower to recover. Our findings suggest that the pronounced sensitivity of K_r to drought is a common feature among different plant species, but recovery may vary depending on root type and water stress severity. K_r dynamics are proposed to modulate g_c response during and following drought.



Session 4-P2 - Peripheral hydraulics

Increased vein and stomatal density do not result in higher photosynthesis unless accompanied by higher hydraulic efficiency in tomato

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Auxins are known to regulate xylem development in plants, however, their effects on water transport efficiency are poorly known. Here we used tomato plants of the *diageotropica* mutant (*dgt*), which has impaired function of a Cyclophilin 1 cis/trans isomerase involved in auxin signaling, and its corresponding wild type (WT) to explore its effects on plant hydraulics and leaf gas exchange. The *dgt* mutation increased the vein and stomata density, which could potentially increase photosynthesis. Nevertheless, even presenting the same photosynthetic capacity of WT plants, the *dgt* showed a photosynthetic rate c. 25% lower, coupled with a stomatal conductance reduction of 52%. The xylem conduits of *dgt* showed a reduced hydraulically-weighted vessel diameter (D_h) (24-43%) and conduit number (25-58%) in petioles and stems, resulting in lower theoretical hydraulic conductivities (K_t). On the other hand, no changes in root D_h and K_t were observed. The measured stem and leaf hydraulic conductances of *dgt* agreed with the K_t values and were lower (up to 81%) than the WT as well; however, despite *dgt* and WT showed similar root D_h and K_t , the measured root hydraulic conductance of *dgt* was 75% lower. These results clearly demonstrate that increases in D_v and D_s only result in higher leaf gas exchange when accompanied by higher hydraulic efficiency in tomato.



Session 4-P3 - Peripheral hydraulics

Drought and temperature interaction on leaf hydraulic traits in grapevine

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Global warming and increased frequency and/or severity of drought events are among the most threatening consequences of climate change for agricultural crops. Understanding the mechanisms of plant responses to both stressors is pivotal to successfully implement management strategies. Here we explored the effect of temperature on the development of grapevine leaves with particular focus on hydraulic traits under well-watered and water deficit conditions. We grew grafted grapevine (*Vitis vinifera* L. cv. Pinot noir) in two different greenhouse chambers (20/15°C vs 25/20°C day/night) and monitored their gas exchange, leaf size, stomatal density, chlorophyll fluorescence, pressure-volume (PV) curves, osmotic potential and petiole xylem anatomy. PV curves provided clear evidence that both, temperature and water availability, strongly affected the turgor loss point (TLP) as well as the connected physiological traits. Leaves developing at higher temperature exhibited a more conservative behaviour characterised by a lower $g_{s \max}$ and a tighter stomatal closure in response to drought. The study further discusses the results considering the coordination of traits changing in tandem and implications in the face of climate change.

Key message: The ambient temperature at which leaves develop impacts on its hydraulic traits and therefore on their successive response to drought

Session 4-P4 - Peripheral hydraulics

The petiole xylem structural traits in *Ulmus laevis* seedlings correlate better with leaf gas exchange traits during drought stress than under well-watered conditions

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It was shown that the petiole xylem structure could be an important predictor of leaf gas exchange capacity, but the question of how petiole xylem structure relates to leaf gas exchange under different environment conditions remains unsolved. Here, we investigated the intraspecies coordination of leaf gas exchange and petiole xylem traits in two-year old seedlings of *Ulmus laevis* Pall. during well-watered and drought conditions. It was found that all studied petiole xylem traits of the elm seedlings were positively correlated with each other. This shows that the development of petiole xylem structure is internally well-coordinated. Nevertheless, the lower correlation coefficients between some petiole xylem traits indicate that the coordination is also individually driven. Drought stress shifted the relationships between physiological traits. Moreover, there were more structure-function relationships under stress conditions. This indicates the importance of petiole xylem structure in dictating the water loss during drought stress. Although several structural-functional traits were related, the range correlation coefficients indicate that the internal coordination between structural-functional traits differs substantially between individual elm seedlings. These findings are very important in the context of expected climatic change, as some degree of intraspecies variations in structure-function relationships could ensure the survival of some individuals under different environmental conditions.

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Session 4-P5 - Peripheral hydraulics

Reproductive water supply is prioritized during drought in tomato

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Reproductive success largely defines the fitness of plant species. Understanding how heat and drought affect plant reproduction is thus key to predicting future plant fitness under rising global temperatures. Recent work suggests reproductive tissues are highly vulnerable to water stress in perennial plants where reproductive sacrifice could preserve plant survival. However, most crop species are annuals where such a strategy would theoretically reduce fitness. We examined the reproductive strategy of tomato (*Solanum lycopersicum* var. Rheinlands Ruhm) to determine whether water supply to fruits is prioritized above vegetative tissues during drought. Using optical methods, we mapped xylem cavitation and tissue shrinkage in vegetative and reproductive organs during dehydration to determine the priority of water flow under acute water stress. Stems and peduncles of tomato showed significantly greater xylem cavitation resistance than leaves. This maintenance of intact water supply enabled tomato fruit to continue to expand during acute water stress, utilizing xylem water made available by tissue collapse and early cavitation of leaves. Here, tomato plants prioritize water supply to reproductive tissues, maintaining fruit development under drought conditions. These results emphasize the critical role of water transport in shaping life history and suggest a broad relevance of hydraulic prioritization in plant ecology.



Session 4-P6 - Peripheral hydraulics

Genetic constraints on cell and tissue anatomy in the C4 grass *Panicum virgatum*

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Grasses operating the C4 biochemical pathway dominate tropical and subtropical grasslands and savannas and account for a quarter of terrestrial primary production. The pathway, which minimizes photorespiration by concentrating CO₂ near the site of ribulose-1,5-biphosphate carboxylase-oxygenase activity, has independently evolved across 62 lineages. Essential to the success of this biochemical innovation is a syndrome of anatomical structures that facilitate the separation of the light and carbon reactions. In many lineages, C4 photosynthesis can be attributed to a single developmental change in vein density. Recent studies have focused on molecular processes regulating vascular development. Less well studied, however, is the architecture of the path of exchange across the leaf lamina, though this is a major source of resistance to diffusion of CO₂ and is central to the efficiency of C4 photosynthesis. Moreover, physical constraints on cell and tissue geometry based purely on mesophyll conductance and gas exchange, or pleiotropic constraints regulating the allometric expansion of cells, could act as barriers to breeding programs. Here we use two genetic mapping populations of the C4 grass *Panicum virgatum* to establish the drivers of scaling allometries for functionally significant anatomical traits. We identify pleiotropic relationships between loci associated with cell size and shape across tissues, explore the independent and interactive effects of polyploidy, population demography, and climate on cell and tissue anatomy, and relate these trends to whole plant performance.



Session 4-P7 - Peripheral hydraulics

Leaf water uptake and daily xylem sap composition in two mangroves

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Mangroves are highly salt-tolerant species living exclusively in intertidal, saline environments. Though, they still rely on non-saline water to maintain hydraulic integrity and plant productivity. Leaf water uptake (LWU) is known to support plants with limited access to rain and ground water sources.

We investigated the dynamics of LWU in *Avicennia marina* and *Aegiceras corniculatum* by submerging and spraying excised branches and measuring leaf water potential (Ψ) at different time intervals. We also analyzed daily changes in xylem sap composition (osmotic potential, ionic concentrations, electrical conductivity, pH and surface tension) during two days characterized by the presence of morning dew and opposite tides.

LWU occurred over relatively short times in both species. Ψ recovered from -4.5 MPa to ca. -1.5 MPa in 120-150 min in both submerged and sprayed branches. At predawn, Ψ was higher (-1.5 MPa) than sea water Ψ , indicating that leaves had been partially rehydrated by absorbed dew. Tides did not affect Ψ , but high tides increased the overall ionic content of xylem sap. Changes in xylem sap surface tension were also related to tide height and ions.

Results indicated mangroves are extremely efficient in absorbing non-saline water and restoring the water favorable balance to Ψ higher than sea water. Tides and consequent changes in xylem sap composition do not affect LWU.

Key message: Mangroves exhibited fast leaf water uptake and water potential recovery. High tides affected the overall ionic composition of xylem sap but did not affect early morning dew uptake.

Session 4-P8 - Peripheral hydraulics

Relations between stem water potentials, stomatal conductance and photosynthesis in three woody species grown in Mediterranean environment

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With climate change and decreased water supplies, interest in more water-efficient irrigation scheduling that consider plant physiological response to drought is increasing. However, define specific plant based water stress thresholds may be difficult due to the large genotype-specific response to water availability. The objective of this study is to compare the relation between stem water potential (SWP), stomatal conductance (g_s) and photosynthesis (P_n) for three Mediterranean species, Olive, Pistachio and Almond.

Olive reached the lowest hydration levels, with SWP values decreasing to -4.0 MPa that correlated well and exponentially with leaf gas exchanges, highlight the strong control of stomatal on water lost in this species. Pistachio showed gas exchange reduction at SWP below -2 MPa but when the SWP was between -1 MPa and -2 MPa this species showed a dual behavior, with some less water-efficient leaves showing extremely high values of g_s (900 mmol m⁻² s⁻¹) corresponding to the highest P_n (30-25 μ mol m⁻² s⁻¹), and more water-efficient leaves with 65% lower g_s values and only 35% lower P_n . Almond had highest level of hydration in the field condition considered and the different parameters measured were poorly related, suggesting a tendency to close stomata to maintain better hydration under water scarce condition.

The implication of these differences in water relations is discussed from a physiological approach and in the prospective of improving water productivity in irrigated agriculture.

Experimental test of the hydraulic disconnection hypothesis in the phenomenon of physiological reddening of Douglas-fir

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Young Douglas fir, *Pseudotsuga menziesii*, has been subject to frequent winter physiological reddening of the needles leading to their dieback. Based on bioclimatic analysis of the phenomenon, hydraulic failure combined with photo-oxidative stress has been hypothesized to induce physiological reddening. An excessive water loss through transpiration during unseasonably warm temperatures spells, combined with reduced water uptake due to low soil temperature, could induce hydraulic failure in the needles. Excessive light in dehydrated plants can induce photo-oxidative stress, damaging needles.

To test these hypothesis, Douglas-fir saplings were exposed to cold soil (ca. 3°C) and warm air (>18°C) in greenhouse. A subset was exposed to high light intensity to induce photo-oxidative stress. Low soil temperature induced a limited root water uptake that triggered stomatal closure, low but steady water potential and limiting growth. High thermal amplitudes between the below- and above-ground parts, even combined with high light influence were not sufficient to induce physiological reddening of Douglas-fir saplings. However, these conditions may only promote higher vulnerability although the physiological trigger has yet not been identified.



Session 5-P1 - Concepts and methods

Water loss from bagged leaves

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In ecophysiology, the water potential (Ψ) of bagged leaves is considered constant, and leaves are thus commonly kept in bags for hours before their Ψ is measured. We hypothesized that water is lost from the leaf to the bag surface due to the leaf's metabolic heat evolution, resulting in a substantial Ψ drop through time.

We explored the rate of Ψ drop in bagged leaves under various conditions while measuring the water loss to the bag (by weighing the increase in the empty bag weight) or to the atmosphere (by weighing the decrease in bag+leaf weight) for six hours. We've also used a simple energy balance model to simulate a wide range of conditions.

We found a significant Ψ drop of up to 0.15 MPa/h where ~65%-85% of the water that was lost from the leaf condensed on the inner bag surface. The Ψ drop rate was higher in plastic bags than in aluminum bags due to higher vapor conductance and also a higher condensation rate in the plastic bags. The Ψ drop rate was also higher in leaves with initially higher Ψ . Keeping the bags under 4° C reduced the Ψ drop by 70%. We also found that the leaf is hotter than the bag by 0.2-0.3 °C, probably due to its metabolic heat evolution. The energy balance model showed that the rate of water loss is significantly decreased under cool room conditions, low stomatal conductance, and initially low Ψ .

The findings highlight that keeping bagged leaves for long periods before they are measured could lead to erroneous estimation of Ψ .

Session 5-P2 - Concepts and methods

Cross-validation of Psychrometer and Scholander water potential measurements

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Measurements of water potential (WP) are crucial in analyses of plant water relations. Two standard techniques for WP determination are the Scholander chamber and psychrometry, though studies comparing both methods are scarce. Here we analysed the congruence of Scholander and psychrometric measurements on leaves of six species.

Branches of three conifers and three broadleaved species were dehydrated on the bench in a range between 0 and -5 MPa. In intervals, WP on cut leaves or terminal shoots were measured with a PMS pressure chamber. In parallel, discs of leaves or several needles, were enclosed in C52 chambers and the WP determined with a PsyPro system. PsyPro WP values were manually converted from microvolt readings based on previous calibrations via standard solutions.

Correlation of Scholander and psychrometric measurements varied across species ($r^2 = 0.41$ to 0.91 ; deviation 0.13 ± 0.1 to 0.61 ± 0.1 MPa). In most species, both methods corresponded well in moderate WP ranges (-1 to -3.5 MPa, deviation 0.08 ± 0.1 to 0.3 ± 0.1 MPa), while at low WP Scholander values were often lower than psychrometer values.

Psychrometric measurements enabled accurate measurements in many species, especially in moderate WP ranges, and thus are a useful alternative (e.g. for small samples, seedlings) to the Scholander method. We recommend careful system calibration and measurements of psychrometer versus Scholander curves for accurate WP monitoring.



Session 5-P3 - Concepts and methods

X-ray MicroCT causes minor impacts on the physiology of living plants in the medium term but can distort manipulative experiments in the long term

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Micro-computed tomography (MicroCT) is a non-destructive imaging method used in plant sciences utilizing X-rays to visualize *in situ* plant tissues and structures and to facilitate quantitative assessments of the loss of xylem conductivity. Few studies used MicroCT in long-term experiments, whereas evidence for cellular damage caused by X-ray MicroCT has been shown recently. Overall, the impacts of X-rays on plant physiological functions are not well understood, while these are particularly relevant for studies that aim at tracking embolism changes *in situ* in trees and could question the results gathered in long-term manipulative studies. The consequences of non-visible damages to processes such as carbon and water uptake and transport are virtually unknown but likely dependent on the parameters used during MicroCT scans (i.e., intensity, power, scan time, filters). The study assessed how X-rays impact the physiology of plants (gas exchange, growth, chlorophyll content, carbon allocation and transport, embolism) to better consider the use of MicroCT in experiments lasting one growing season. We showed that monthly application of X-rays reduced the radial growth of tree stems but had little impact on other physiological traits if the exposure did not exceed one growing season.

Key message: X-ray MicroCT has no adverse effect on plant physiology and thus proves to be a reliable method for tracking plant embolism in short-term experiments.



Session 5-P4 - Concepts and methods

Undersaturation artifacts cause severe overestimation of relative water content

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A new mortality framework for woody-plant death highlights water flows and pools as central cornerstones for plant function. Recent studies have also highlighted the usefulness of water content as a predictor of tree death because it can be remotely sensed through canopy spectral reflectance. Among the different measures of plant water content that exist, the relative water content (RWC) has gained popularity because its relative nature allows us to compare plants with different morphologies and absolute water contents. However, this measure requires accurate values of the saturated water mass of tissues to relativize values, usually obtained by rehydrating tissues. However, rehydration can cause both, over- and under-saturation artifacts, the latter of which has received little attention. Oversaturation artifacts have been extensively discussed in the literature, but undersaturation artifacts have received less attention. Here, we show that undersaturation artifacts lead to overestimation of up to 50% in RWC values. The degree of overestimation depends on both leaf morphology and level of dehydration. We propose two alternative methods to obtain saturated water content that overcome this issue. Spectral reflectance models support the use of these alternative methods over the classic RWC approach.

Key message: Undersaturation artifacts cause severe overestimation of relative water content.



Session 5-P5 - Concepts and methods

Advanced imaging and quantification of the cambium and developing xylem in eucalypts using X-ray micro- and nano-computed tomography (CT)

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The formation of xylem (xylogenesis) occurs in the cambium and a narrow zone of subsequent differentiation, both of which play key roles in plant growth and development. However, the dynamics of xylogenesis remain poorly understood, largely due to challenges in sampling, imaging and characterising properties of the cambial and differentiating tissue. Being able to see and make measurements of cambial tissue are generally done by taking samples, always from a different location, which means the same cells are not being monitored. In this study, therefore, we explore the potential to use X-ray computed tomography (CT) to characterise and quantify the cambium tissue at high resolution in eucalypts. We present a workflow to evaluate changes in dimensions of the zone of xylem differentiation in small trees exposed to irrigated and droughted conditions. To track cambium microstructural changes, the same point in the cambial zone on the same plants were scanned with non-destructive X-ray μ CT, at a resolution of 9 μm , before and after the respective treatments. Additionally, high-resolution X-ray nano-CT was employed, where a sub-sample of the stem was scanned at a resolution of 1.25 μm . Using image analysis techniques, the morphological characteristics of the cambium tissue could be determined. X-ray CT provided a very distinct visual insight into the cambium structure, demonstrating clear differences between the two treatments.

Key message: X-ray CT demonstrated to be a valuable tool for examining the effect of changing environmental conditions on the cambium structure and cell morphology.

Session 5-P6 - Concepts and methods

Stomatal optimality during drought: Theory and observations

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Under water stress, the link between stomatal regulation and soil-plant hydraulics is critical for predicting water use regulation of plants. Many models follow the stomatal optimality theory which states that plants optimize the trade-off between carbon gain and cost of transpirational water loss when opening their stomata. Stomatal optimization models are widely used, however, they often lack systematic experimental evidence and deliberately ignore the underlying stomatal mechanisms. Here we present a series of experiments in which the hypothesis on the optimality of carbon assimilation over transpirational water loss is systematically tested. We simultaneously measured assimilation rate, stomatal conductance and leaf water potential in plants exposed to varying light intensity, vapor pressure deficit and soil water content. Additionally, we systematically manipulated the leaf water potential by pressurizing and depressurizing the soil-root system. The results provided new evidence on the response of stomatal conductance to assimilation rate and leaf water potential. We explained the data with a model in which stomatal conductance is function of the ratio between assimilation and leaf water potential. The model explains how plants efficiently regulate transpiration to avoid excessive, nonlinear drops in leaf water potential by adjusting stomatal conductance to soil hydraulics and atmospheric conditions. Although the model does not necessarily presuppose stomatal optimality, it results in stomatal behaviour similar to optimization models.



Session 5-P7 - Concepts and methods

A mobile small-scale MRI scanner and complementary imaging method to visualize embolism formation and measure xylem hydraulic vulnerability

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Non-invasive imaging has had a large impact on the study of embolism formation in plants and trees. Currently only two methods allow non-invasive imaging of emboli in cross sections of stems: micro CT and MRI. So far both methods required sizeable, costly machines, which are mostly restricted to the lab and only accept potted plants of limited size. In this contribution we demonstrate how for MRI these limitations have been overcome.

A number of key issues have restricted the use of MRI to image embolism formation until now: mobility of the instruments, varying environmental conditions, cost of purchase and maintenance, inability to image large trees, and the detection of emboli in conduits smaller than can be spatially resolved. To address these issues we built mobile, small-scale MRI scanners, based on permanent, low field MRI magnets which do not require power or cryogenic cooling. We ran these devices with an efficient imaging sequence, capable of acquiring quantitative images (parameter maps) of water content and water mobility. We show that these images can be used to distinguish filled and cavitared xylem conduits in beech, even if these are ten times narrower than can be spatially resolved. A multiplication of parameter maps of water content and water mobility was shown to yield images in which filled xylem appeared with even greater contrast than in the two parameter maps separately. These small-scale MRI devices thus enable straightforward visualization of the spatial and temporal dynamics of embolism formation, and the calculation of vulnerability curves.

Session 6-P1 - Drought-induced tree mortality

To save water or not to save, that is the question: tree-ring stable isotopes explain the dieback of *Quercus ilex* in southern Tuscany (Italy)

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Quercus ilex L. dieback has been recently observed on the southern coast of Tuscany (Italy). The research was carried out in two stands with different levels of dieback, a declining *Q. ilex* stand (D), where 80% of the trees exhibited crown-defoliation and dead branches, and a non-declining one (ND) (dieback affected 20% of the trees) located 1km from each other. We hypothesized that different damage levels are connected to different strategies to cope with drought stress. Dendrochronological and tree-ring $\delta^{13}\text{C}$ analyses were applied to investigate the impact of two major drought events (2012 and 2017) on *Q. ilex* growth and water use efficiency (WUE). Overall, D showed a lower growth rate than ND. Furthermore, $\delta^{13}\text{C}$ was significantly reduced in D than in ND from 2000 to 2020, highlighting a more water-spending strategy for *Q. ilex* in D. Drought events in 2017 significantly decreased growth in D, while this effect was not observed in ND. Drought event in 2017 was stronger than in 2012, as shown by the increased WUE revealed by tree-ring $\delta^{13}\text{C}$. Our results suggest that the differences in *Q. ilex* dieback in the two stands could potentially be linked to the different water-use strategies adopted. A more conservative use of water may have helped *Q. ilex* to cope with drought in ND and to maintain a higher growth rate compared to D.

Key message: Different levels of *Quercus ilex* dieback observed in two close stands could be linked to the different water strategies adopted.

Session 6-P2 - Drought-induced tree mortality

Mild drought treatments prime the recovery from severe drought by modifying the tradeoff between non-structural carbohydrates and growth in black poplars

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Plant recovery from drought can rely also on a NSC pool implied in the restoring of water transport. We hypothesized that mild drought treatments can prime a faster recovery of plants experiencing a further severe drought, as consequence of the trade-off between NSC accumulation and plant growth. One set of *Populus nigra* plants were exposed to two cycles of mild drought treatments followed by a severe water stress and drought relief, while a second group underwent only a severe drought and recovery. Poplars exposed to priming treatments showed a reduced growth and a higher NSC content in bark, wood and xylem sap compared to not primed plants. During drought, both groups of plants displayed similar loss of hydraulic conductivity (PLC). Although, after 5 hours of stress relief, both groups showed a recovery of xylem pressure, only a partial drop in the level of PLC was measured. However, the primed poplars exhibited a higher level of hydraulic recovery compared to not primed plants. During drought and recovery, the NSC content in bark and xylem sap increased in both groups, being significantly higher in primed than untreated poplars. The primed plants exhibited, during stress, a higher NSC/plant DW and, during recovery, a starch decrease. We suggest that the reduction of plant growth, as a consequence to priming, leads to the formation of a pool of sugars that can allow a faster and more effective recovery of xylem functionality.

Key message: drought priming in poplar relies on the tradeoff between Non-structural carbohydrates (NSC) reserves and plant growth.

Session 6-P3 - Drought-induced tree mortality

The role of stem diameter in tree hydraulics – insights from pure and mixed stands of European beech and Douglas fir during four consecutive years

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In forestry, stem diameter changes were traditionally considered unidirectional: every year, a new growth ring is formed. However, on a smaller time scale, stem diameter can tell much more, including the current water status of the tree – data that is delivered by high-resolution dendrometers. Since 2018, we have been monitoring stem diameter of pure and mixed stands of European beech and Douglas fir in north-western Germany with a 10-minute resolution. Despite individual differences, we found species-specific patterns in growth as well as in tree water deficit. Notably, these species-specific patterns also differed between pure and mixed stands. Our data suggests that mixing European beech and Douglas fir has a positive effect on the water status of both species, thus pointing to a higher stand drought tolerance.

Key message: Tree water deficit derived from high-resolution dendrometers indicates that mixing European beech and Douglas fir has a positive effect on stand drought tolerance.



Session 6-P4 - Drought-induced tree mortality

Conifer desiccation in the 2021 NW heatwave confirms the role of hydraulic damage

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The unprecedented heatwave which hit the Pacific northwest of North America in late June–early July 2021 impacted ecosystems and communities, yet evidence for and analysis of this impact are still missing. Here we bring a unique dataset quantifying the impact on conifer trees, which are keystone species of many northwest ecosystems. Moreover, we take advantage of this exceptional event as a broad, extreme, ‘field experiment’ to test a fundamental theory in plant physiology and prepare our forests for a harsher future. Overall, the data collected confirm the role of hydraulic vulnerability in drought-induced injury to trees.

Session 6-P5 - Drought-induced tree mortality

The dependency of plant water status regulation on drought tolerance traits in five temperate tree species differing in their degree of isohdry

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Stomatal regulation of plant water potential (ψ_x) is paramount to understand species ability to survive under increasing drought stress. The degree of stomatal stringency can be framed into the isohdry-anisohdry continuum representing the two extremes of plant water regulation strategies. Here, we determined how plant hydraulic traits vary along this continuum, and characterized water status regulation of five temperate tree species differing in their degree of isohdry. Among other traits, we estimated water potential at stomatal closure (ψ_{s90}), turgor loss point (ψ_{tlp}) and xylem safety (ψ_{50} and ψ_{88}), hydroscape area (HA), hydraulic safety margin (HSM; calculated as $\psi_{s90} - \psi_{88}$), shoot water capacitance (C_{shoot}), and time to hydraulic failure (THF) obtained from drying out experiments on saplings. We expect species degree of isohdry to be associated with HA and HSM, with more isohdryic species having larger HA and HSM, while the time to hydraulic failure will be related to HA, HSM, xylem safety and C_{shoot} . Furthermore, we assume C_{shoot} to be well related to xylem safety and species water status regulation. We consider this a step towards the understanding of plant hydraulic strategies across species, highlighting the importance of overlooked hydraulic traits such as C_{shoot} and ψ_{s90} to define species ability to mitigate rising drought events.

Session 6-P6 - Drought-induced tree mortality

How stem diameter of Scots pine and Norway spruce responds to different temperature treatments in the winter

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The climate into which boreal conifers have adapted to is changing. Global mean temperature is increasing, which lengthens the time period in the autumn and in the spring when temperature is close to zero and trees face frequent freezing and thawing events. It is important to investigate the physiological consequences of these events. In this study, we subjected pine and spruce saplings to 90 temperature cycles in a test chamber. Each cycle was 4 hours long. Temperature was first decreased by 6°C and then increased by 6°C with a change rate of 6°C/h. We had 3 different treatments with different temperature ranges: control (+10°C/+2°C), freeze-thaw (+2°C/-4°C) and sub-freezing (-2°C/-10°C). Total of 6 experiments were conducted; two replications of each treatment. We monitored stem diameter dynamic in saplings during the experiments to gain information about water relations, freezing processes and freezing injuries. Response in saplings from the three treatments was clearly different. Amplitude of stem diameter change per temperature cycle was high on the freeze-thaw and sub-freezing treatments, but negligible in the control treatment. Saplings also experienced gradual shrinking in diameter from one cycle to another. This shrinking was the highest in the sub-freezing while minimal in the control treatment. We also analyzed freezing temperature (FT) for saplings. FT was always much lower in the first cycle than in consequent cycles. FT of saplings correlated with needle water potential.

Key message: Stem diameter dynamics can be very different during winter depending on temperature.



Session 6-P7 - Drought-induced tree mortality

Stem photosynthesis: an ally for trees facing drought?

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We characterized the photosynthetic apparatus of bark and wood chloroplasts in *Fraxinus ornus* L. (*F.o.*). Blue light was mainly absorbed by the outer bark, and far-red enriched light reached the xylem and pith. The stem (bark and wood) photosynthetic apparatus was apparently acclimated to the red-enhanced and low-light environment, as shown by higher amounts of LHCII, PSII, more abundant grana, less PSI and stromal thylakoids compared to leaves. We demonstrate that, despite receiving limited light intensity, and also enriched in red wavelengths, stem chloroplasts are fully photosynthetically active.

We then verified if inhibition of stem photosynthesis increases plant vulnerability to drought, by covering stems of *F.o.* saplings with aluminum foil for 30 days. Plants were then subjected to water stress down to leaf water potentials of -3.5 MPa and then re-watered to quantify their recovery capacity. Data revealed that the lack of stem photosynthesis affected the hydraulic response during a drought event, but did not affect the recovery phase.

Finally, we conducted a wider screening of quantum yield of PSII (F_v/F_m) at bark and wood level among Angiosperm species with different vulnerabilities to xylem embolism (P_{50}). We show that species more resistant to drought also displayed higher values of bark F_v/F_m , reinforcing the hypothesis of a possible role of stem photosynthesis in drought stress responses.

Key message: Stem photosynthesis can provide an extra carbon gain that might help woody plants to cope with the detrimental effects of drought.

Session 6-P8 - Drought-induced tree mortality

Influence of soil moisture on stomatal conductance and drought resistance in European beech, Norway spruce and Douglas-fir over a growing season – Insights from juvenile tree experiment

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The increased frequency and intensity of hotter droughts have amplified the susceptibility of trees to hydraulic failure and carbon starvation, potentially resulting in mortality. To support future silvicultural decisions, it is important to understand species-specific tolerance and adaptation potential to increasing drought events. We chose three silviculturally important tree species, the native *Picea abies* (PA) and *Fagus sylvatica* (FS) and a non-native *Pseudotsuga menziesii* (PM). The water and nutrient availability of tree saplings was varied. We measured plastic ecophysiological traits such as stomatal conductance (G_s), hydraulic safety margin and turgor loss point (TLP) multiple times during the growing season. Further, we measured biomass, leaf cuticular conductance (g_{min}) and xylem pressure at 50% (P_{50}) and 88% (P_{88}) loss of hydraulic conductivity. Considerable adjustments in stomatal conductance and TLP were visible in all three studied species over the growing season. The g_{min} was considerably higher in beech compared to the two conifers. TLP, P_{50} and P_{88} were similar in all three species. Lower water availability resulted in reduced stomatal conductance and a quick dry down of the plants which was prominent in FS. FS, PM, and PA showed anisohdry, moderate isohdry, and strong isohydric behaviour, respectively. Despite the observed similar drought resistance in all the studied three species, the noticeable higher biomass in PM, highlights it as a promising replacement species for PA.

Session 6-P9 - Drought-induced tree mortality

The time required to cross the stomatal safety margin varies between species and leads to differences in survival to drought

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The plants' ability to regulate water loss and the propagation of embolisms in xylem vessels have usually been investigated individually. The development of an integrated approach considering the temporal dynamics and relative inputs of these mechanisms to plant drought responses is urgently needed. Seedlings of three highly embolism-resistant species, *Cupressus sempervirens* L., *Juniperus communis* L. and *Tetraclinis articulata* (Vahl) Mast., and one embolism-sensitive *Taxodium distichum* (L.) Rich., were screened during the plant dehydration. The four main traits related to drought survival: turgor loss point, stomatal closure, minimum leaf conductance and xylem embolism resistance, were measured. All species reached full stomatal closure before the onset of embolism, with all but the most drought-sensitive species presenting large stomatal safety margins, demonstrating that highly drought-resistant species do not keep their stomata open for longer in drought conditions. Time to death was significantly influenced by xylem embolism threshold, stomatal safety margin, and minimum leaf conductance. We introduced an integrated trait, the stomatal margin retention index (SMRI_{ψ50}), which considers the thresholds of stomatal closure and hydraulic failure, together with the rate of desiccation. The SMRI_{ψ50} showed the best explanatory power for mortality variance during drought than any other hydraulic trait and might become a key tool for predicting shifts in species distribution under climate change.

Key message: The SMRI_{ψ50} is a novel integrated index to predict drought survival in plants.

Hydraulic and metabolic responses of *Pinus sylvestris* to heat and hot drought events, and subsequent stress release

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Forests will increasingly be affected by heat events, often cooccurring with drought. To improve our understanding of tree resilience, we investigated the impacts of a heatwave on hydraulic and metabolic processes in well-watered and drought-treated Scots pine seedlings, followed by recovery trajectories. Individual chambers served to continuously measure above- and belowground CO₂ and H₂O gas exchange, and stem diameter change. Further, indicators of stress impact and recovery capacity were analyzed.

Well-watered Scots pine seedlings mitigated heat stress by increased transpiration rates, while leaf temperatures of drought-treated seedlings reached 46°C, resulting in larger metabolic and hydraulic impairment. Under drought-heat, carbon (C) uptake strongly declined and needle water potential reached –2.7 MPa, alongside a 90% decline of leaf hydraulic conductance (K_{Leaf}). Heat alone resulted in low functional impairment and measured parameters recovered fast. While drought-treated seedlings also survived and quickly recovered the whole-tree net C balance, K_{Leaf} did not fully recover and stem hydraulic conductivity remained 25% below controls. This indicates a new equilibrium of C uptake and release independent of hydraulic impairment. However, incomplete hydraulic recovery leaves the seedlings vulnerable to subsequent heatwaves.

Key message: Heat stress (max. 42°C) in drought-treated Scots pine seedlings resulted in large hydraulic and metabolic impairment. Post-stress, the whole-tree net carbon balance recovered fast, while the recovery of the hydraulic system was incomplete.

Session 6-P11 - Drought-induced tree mortality

Critical water contents at leaf, stem and root level leading to irreversible drought-induced damage in two woody and one herbaceous species

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Climate warming has produced severe damage to forests and crops, including reduction in productivity, plant decline and death. Increasing interest into alarming plant die-off events has demonstrated that drought-driven tree mortality might be caused by two interrelated physiological mechanisms: hydraulic failure and negative plant carbon balance. Despite substantial efforts, however, the availability of simple and reliable indicators of mortality risk is still scarce. Measurements of relative water content (RWC) have been proposed as a possible tool for monitoring the risk of drought-induced plant failure. However, different questions are still unresolved, including the identification of critical thresholds leading to cell damage and plant failure. The present study was aimed at identifying the critical water content thresholds leading to irreversible plant damage and increased mortality risk in three species with different leaf habits and growth forms (i.e., the herbaceous *Helianthus annuus* and the woody species *Populus nigra*, a deciduous tree, and *Quercus ilex*, an evergreen tree). Our findings suggests that RWC = 50% induced severe damage to cell membranes, hampering the rehydration capacity and paving the way to plant death, in all the measured species. Our findings provide data supporting the use of remotely-sensed vegetation water content for large-scale monitoring of the risk of mortality of forests and crops.

Session 7-P1 - Xylem structure and function

Sap flow as a main driver of xylogenesis within drought-affected Norway spruce and Scots pine at middle altitude

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The water balance becomes a significantly important key factor determining the course of tree secondary growth. The dry periods result in fluctuated level of daily sap flow (SF) of tree stem. This study is focused on how the pine and spruce trees undergo the xylem cell differentiation in multiple-peaked SF during the growing season. We monitored the xylo-morphogenesis of Scots pine (Soběšice – 404 m a.s.l.) and Norway spruce (Rájec – 625 m a.s.l.) trees using weekly micro-core sampling during the whole growing season (March–November; 2013–2016). The sampled trees were equipped with trunk segment heat balance sensors for SF sense. The xylogenesis was analyzed through the permanent microscopic slides where the cambial division and xylem cell differentiation (cell enlargement, wall-thickening and lignification) were evaluated. The analysis of cell enlargement, wall-thickening and the fully formed cell dimensions (cell radial diameter – RD and cell-wall thickness - CWT) was performed. We found that tracheid dimensions, as well as rate of cell enlargement and wall-thickening of both pine and spruce trees are directly affected by SF level. Our study points out that the xylogenesis is a process highly vulnerable to changes of tree transpiration and thus it provides us a clear explanation how the SF is predetermining the xylem cell formation, which copes with intra-annual morphological fluctuations. Consequently, we can claim that SF bridging the soil and air conditions plays a role as a growth regulator in coniferous trees.

Session 7-P2 - Xylem structure and function

Hydraulically nonfunctional xylem areas in Alpine shrubs

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The xylem long-distance water transport capacity is a key determinant of plant hydraulic function and paramount for survival and growth of woody species. Plants thus should optimise hydraulic conductance while minimizing the risk of temporary or permanent conduit dysfunctions. Here we show that Alpine (dwarf) shrubs of the family Ericaceae frequently exhibit persistent xylem dysfunctions during the vegetation period without being exposed to drought stress. Nonfunctional areas accounted for 19-50% of the total xylem area in *Arctostaphylos uva-ursi*, *Kalmia procumbens*, *Calluna vulgaris*, *Erica carnea*, *Vaccinium myrtillus*, and *V. gaultherioides*. They occurred in various but regular and species-specific cross-sectional patterns and reduced considerably the specific hydraulic conductivity. However, the lower the functional xylem fraction, the higher was the hydraulic efficiency of conducting xylem areas. The decommission of inner growth rings was clearly related to stem age and higher vulnerability of older rings, while nonfunctional conduits in each annual ring may be caused by freeze-thaw induced cavitations in spring. The latter is topic of additional ongoing investigations of seasonal changes in *Rhododendron ferrugineum* under/above snow. Improved understanding of the vessel functional lifespan and nature of dysfunctions is critical to correctly assess structure function relationships and whole-plant hydraulic strategies.

Key message: Alpine shrubs show high proportions of persistent nonfunctional xylem in the absence of drought, potentially caused by winter stress.



Session 7-P3 - Xylem structure and function

Do environmental conditions affect the variation of conduit and interconduit-pit dimensions within trees?

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Xylem conduits widen with distance from the treetop. The respective scaling of interconduit pits is less well known. Furthermore, the potential influence of growing conditions on conduit and pit dimensions is unclear. Our study aims to shed new light onto the coordination of conduit and pit dimensions at various distances from the treetop and to understand better, if these dimensions can adjust to varying growing conditions. We selected Norway spruce, Scots pine and silver birch trees growing on two sites with different soil types, thus having different growth rates, and took several xylem samples along the water transport pathway from the treetop to the roots. Currently, we are measuring conduit and pit dimensions in these samples. At breast height, spruce had a higher mean tracheid diameter and mean hydraulic diameter, and birch showed a higher mean pit-membrane area, and ratio of pit-aperture area to cell-wall area on the favorable site. Pine showed no differences in conduit or pit dimensions. While spruce and birch were taller on the favorable site, pine was of similar tree height on both sites.

Key message: Our preliminary results suggest, that environmental conditions may influence conduit and pit dimensions *via* the tree height.

Session 7-P4 - Xylem structure and function

Addressing controversies in embolism resistance – vessel diameter relationships

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Although xylem embolism formation is a key process during drought-induced tree mortality, its relationship to wood anatomical properties remains incompletely understood. Traditionally, wider vessels are assumed to be associated with high risk to embolism, but without a direct, mechanistic explanation. Moreover, bordered pit characteristics are known to play a role in embolism resistance. Based on data from 20 temperate broad-leaved tree species, we study across- and within-species relationships between the water potential at 50% loss of conductivity (P_{50}), hydraulically-weighted vessel diameter (D_h), pit membrane thickness (TPM) and specific conductivity (K_s). Both species with thicker pit membranes and larger vessels had a lower embolism resistance. While D_h and TPM were weakly associated, this was not sufficient to explain the observed link between P_{50} and D_h , which remained highly significant after accounting for TPM. The interspecific pattern between P_{50} and D_h was mirrored by a significant link between P_{50} and K_s , but not accompanied by an intraspecific relationship between P_{50} and D_h . Our results provide robust evidence for an interspecific scaling of P_{50} with D_h in 20 temperate angiosperm tree species, and suggest that previous controversies about P_{50} – vessel diameter relationships may arise from differences in the species sample and the level of aggregation on which they are studied.

Session 7-P5 - Xylem structure and function

Effects of limited soil water availability on intervessel lateral contact in temperate angiosperm tree species

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Xylem network connectivity is an important determinant of transport efficiency and resistance to hydraulic failure due to embolism. Under limited water availability, woody species may adjust the structure of vessel network to improve their resistance against future soil drought stress. However, the effects of water scarcity on intervessel lateral contact remain poorly understood. Here, we investigated drought-induced modifications in the xylem vessel network in several angiosperm tree species with a special focus on intervessel lateral contact. Anatomical analyses were performed both in stems of seedlings cultivated under different water availability and annual rings of mature individuals developed during years of low and high drought intensities. In response to drought, a decrease in vessel diameter (up to 20%) and a concomitant increase in vessel density (up to 60%) were observed both in seedlings and mature trees. In contrast, we detected only small and species-specific drought-induced changes in intervessel contact frequency and intervessel contact fraction (up to $\pm 15\%$). The minor adjustments in intervessel lateral contacts were primarily driven by contact frequencies between neighboring vessels (i.e., vessel grouping) rather than by changes in proportions of shared cell walls. Our results demonstrate that intervessel lateral contact in angiosperm tree species is a conservative trait of relatively low plasticity. The high interspecific variability in intervessel lateral contact appears to reflect a wide range of hydraulic strategies developed by angiosperm tree species.

Session 7-P6 - Xylem structure and function

On the structure and mechanistic function of angiosperm pit membranes

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Pit membranes of angiosperms play an important role in plants in maintaining water transport under daily and seasonally changing environmental conditions. Pit membranes are still often considered to be pectin-containing and almost two-dimensional structures with holes up to several hundred nanometres wide. In contrast, it has now been established that the third dimension of the pit membrane, its thickness, is exceptionally well related to embolism resistance and pit membranes should be considered as a meso-porous medium. It has now also been shown that the width of the pore constrictions provides a mechanistic explanation for the correlation between pit membrane thickness and embolism resistance, while the total pit membrane area of a vessel affects embolism resistance much less. These results suggest a decoupling of hydraulic safety and efficiency and a rejection of the rare pit hypothesis in the conventional sense. Consequently, we are examining the relationship between the pit membrane thickness and its hydraulic resistance affecting the xylem sap flowing through. Furthermore, seasonal changes in pit membrane thickness could represent an additional factor in the capacity of plants to adapt to environmental conditions.

Phenotypic variability of xylem cells in hybrid larch crossbred progenies

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Xylem cell characteristics are largely genetically determined. However, depending on site conditions, plant age and location within the tree, the expression of individual characteristics can vary over a wide range. The knowledge about specific wood characteristics is not only important for timber processing, but it is also a basis for the assessment of various physiological processes related to hydraulic architecture of a tree and thus, its capacity to adapt to environmental impacts.

In order to explore the phenotypic variability of xylem cell size, the present research focuses on the characterization of tracheid size of 6 different hybrid larch progenies and one standard European larch from contrasting sites concerning nutrition. The aim of the study was to determine the point of cell length culmination, to investigate the genotype specific variability of cell size, to describe differences between late and early wood and to explore differences between hybrid larch and European larch. **Cell lengths within one and the same tree vary by far significantly. The same is true for individuals within the same progeny.** For each variety and study site cell length increased with cambial age for both, late and early wood cells. Depending on the study site, the juvenile trend culminates at tree age 26 years. Site-specific differences of 3.6 % in a minimum and 13.6 % in a maximum between late and early wood tracheids could be observed. **Concerning cell size, the study indicates a significant heterosis effect for hybrid larch progenies.**

Session 7-P8 - Xylem structure and function

The predictive quality of radial compression strength for vulnerability to cavitation

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Hydraulic testing of isolated sapwood from mature tree trunks is time-consuming and prone to errors, whereas the measurement of compression strength is a standardized and rapid wood technological application. This study aimed to relate compression strength perpendicular to the grain of mature Norway spruce (*Picea abies*) trunk wood to vulnerability to cavitation. The sample-set comprised 52 specimens originating from 34 trees harvested in Sweden. Before mechanical testing, the P_{50} , i.e., the water potential resulting in 50% of hydraulic conductivity loss, was estimated on small sapwood beams employing the air injection method. Compression strength perpendicular to the grain was defined as the first peak of a stress-strain curve (peak stress) when the wood is subjected to radial compression. Peak stress ranged between 1.65 MPa and 5.07 MPa, P_{50} between -3.09 MPa and -1.83 MPa. We found a strong correlation between the peak stress and P_{50} ($r^2 = 0.80$, $P < 0.0001$). This provides further evidence that peak stress in radial compression and P_{50} are both extremely dependent on the characteristics of the “weakest” wood part, i.e., the highly conductive earlywood. We conclude that the radial compression strength is a good proxy for the vulnerability to cavitation of mature conifer trunk wood.



Session 7-P9 - Xylem structure and function

Hydraulics of shrubs growing at Mt. Teide, Tenerife

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The Teide mountain range in Tenerife is characterised by decreasing precipitation above 2000 m. At the treeline ecotone, mean annual precipitation is only about 370 mm. Combined with intense irradiation and respective high temperatures this may lead to drought stress during summer.

In this study, we analysed xylem hydraulic traits of the endemic shrubs Codeso (*Adeonocarpus viscosus*), Teide broom (*Spartocytisus supranubius*) and Rose of Guanches (*Bencomia exstipulata*). Branches, ca. 1m in length, were harvested in the Botanical Garden of the Teide Natural Park and used for analyses of embolism via dye staining, hydraulic safety (vulnerability to embolism) and efficiency k_s (via Cavitron), as well as wood anatomical measurements.

No native embolism was found in study species. The lowest vulnerability to embolism was observed in *A. viscosus* (water potential at 50% loss of hydraulic conductivity $P_{50} = -5.22 \pm 0.13$ MPa), while the other species were comparably vulnerable (P_{50} around -3.5 MPa). The specific hydraulic conductivity was around $10 \cdot 10^{-4} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$, which corresponded to conduit dimensions.

Results do not indicate extraordinary drought stress or respective adjustments in xylem hydraulics, which may be due to deep rooting systems, high water holding capacities in lower substrate layers and low evaporation through volcanic substrate. Increasing summer drought caused by global climate change may thus lead to dieback of Teide shrubs as observed during the last years.



Session 7-P10 - Xylem structure and function

***Pinus sylvestris* L. drought stress reaction thresholds are captured by both intra- and inter-annual variation in xylem morphology**

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As drought-tolerant tree species, *Pinus sylvestris* L. (Scots pine) in Central Europe yet expresses drought-induced secondary growth variability, reflected in cellular and tissue level changes in xylem anatomy. Here, we investigate to what extent Scots pine trees can withstand water deficit stress, and what level of observation better allows to identify it. To study Scots pine xylem formation, 3 research plots (150-350 m asl), representing managed Scots pine stands aged 40-100 years, were selected in the south of the Czech Republic. At each plot, weekly microcore sampling was performed on 6 dominant trees during the growing seasons 2020 and 2021, whereas macrocores were taken from another 12 dominant trees at the end of the study. To relate xylem morphology to climatic variables intra- and inter-annually, we analyzed: i) current timing of tracheid development; ii) morphological metrics of fully formed annual rings, such as tracheid radial diameter, secondary cell wall thickness, and number of tracheids; iii) tree-ring width time series for the whole tree lifespan. Our work aims to identify the numerical thresholds in number, radial dimensions of tracheids and tree-ring widths, up to which these variables can decline without tree dieback. We hypothesize that the same mechanism of drought stress reaction in Scots pine is revealed regardless of tree age, though the information kept by cells and tissues might be different.

Key message: Do both individual tracheids and total tree-ring widths provide the same information on how far Scots pine can withstand drought?



Session 7-P11 - Xylem structure and function

Timeline of earlywood vessel and leaf development in the ring-porous *Quercus lobata* under non-freezing climatic conditions

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Earlywood vessel (EV) formation is thought to precede leaf out in ring-porous trees because they must replace their old EV vessels each spring due to their short functional lifespan. However, this hypothesis has been developed based on data from cold-winter zones, where freezing-induced cavitation can strongly affect large EV of ring-porous trees, but it has not been tested in areas where winter frost is absent. In this study, leaf phenology and EV development were analyzed in *Quercus lobata* Née at an irrigated plot under non-freezing conditions in southern California. Leaf phenology was recorded and wood microcores were weekly collected from eleven trees subjected to different levels of water stress in January-May of 2021 and February-March of 2022. The time when the new EV became functional, as well as prior-year vessel functioning, was evaluated by combining active staining of EV with Crystal violet and microcomputed tomography images obtained from branches in March and April of 2021. Different exposure to water stress was evaluated by measuring leaf water potentials before the onset of leaf coloring. This unique dataset combining different histological approaches and phenological observations allowed us to explore the underpinnings of the environmental control of leaf and wood phenology coordination in ring-porous trees.

Key message: Reduced timelags between earlywood vessel development and budburst in *Quercus lobata* could be related to the presence of functional previous-year earlywood vessels.



Session 7-P12 - Xylem structure and function

Is apex-to-base conduit widening worth a steep axial variation in resistance to drought-induced embolism along the stem in *Abies alba*? Yes!

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What does it make a xylem tissue more or less vulnerable to drought-induced embolism formation? There is a never-ending debate on the existence and significance of a relationship between xylem conduit diameter and the vulnerability to drought-induced embolism in both angiosperms and conifers. In parallel, there is a huge proliferation of studies using conduit diameter as a proxy for xylem efficiency (conductance) and safety (resistance to drought-induced embolism formation). And importantly, there is a persistent and complete neglect of the clear and stable patterns of anatomical traits' variation along the longitudinal axes of stem and branches that likely play a key role for the variation in embolism resistance in the different compartments of a tree.

We assessed the tracheid diameter (TD, pit traits (pit area and aperture) and vulnerability curves (with the air injection method) at different position along the stem of a mature *Abies alba* tree.

We found isometric relationships between tracheid diameter, pit traits, and P_{50} (pressure at which 50 % of conductance is lost). TD and P_{50} scaled with DFA according to a power relationship with exponent of ~ 0.2 . P_{50} varied from 5.5 MPa at DFA= 32 cm to 2.4 MPa at DFA=2500 cm.

In conclusion, resistance to drought-induced embolism formation is highly variable within a tree and highly dependent on the distance from the apex. Therefore, traits like P_{50} cannot be considered key individual traits without accounting for clear path length effects.



Session 7-P13 - Xylem structure and function

Different drought response strategies in six *Arabidopsis* accessions with contrasting stem lignification

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The mechanisms underlying drought-induced embolism are still poorly understood and mainly focus on the relations between P_{50} and xylem anatomical characters. In this study, we complemented and extended the stem anatomical- P_{50} dataset from our previous work in *Arabidopsis* into a broader drought response perspective. We performed a drought experiment on six *Arabidopsis* accessions with contrasting stem lignification in which we measured stomatal conductance (g_s) and leaf water potential (Ψ_l) and calculated the hydraulic safety margin (HSM). Moreover, we compared the expression of four drought-responsive genes from the ABA-(in)dependent (*ABI2*, *AREB1*, *RD29A*, *DREB2A*) pathways to assess levels of drought stress at the end of the drought experiment. We found a considerable difference in drought response among all accessions studied. The most tolerance accessions have the thickest intervessel pit membranes and exhibit the largest HSM. In addition, they keep Ψ_l stable during the water shortage period and show the lowest expression levels of drought-responsive genes. Our results indicate that stem anatomical and ecophysiological leaf traits are intertwined to acquire a certain level of drought tolerance at the whole plant level, and each accession uses a specific combination of traits to cope with drought.

Session 7-P14 - Xylem structure and function

The combined effect of light availability and drought on the survival and ecophysiology of two forest understory herb species

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A dense forest canopy improves the understory microclimate by lowering the temperature. On the other hand, low light availability under dense forest constraints photosynthesis. Here we assessed the survival and ecophysiology of two visually similar perennial herbs of forest understory: isohydric *Asarum europaeum* and anisohydric *Hepatica nobilis*. We grew them under 10% and 1% of outdoor light. Half of them were subjected to water stress until 50% mortality. After the drought, we watered the plants and let them recover. The lowest predawn Ψ was -3.6 MPa, and the midday Ψ were -5.4 and -8.1 MPa for *Asarum* and *Hepatica*, respectively. The two herbs plastically adjusted their A_{sat} to the light environment, so that A_{sat} of shaded *Hepatica* was 38% and of shaded *Asarum* by 29% lower than in controls. After the drought A_{sat} of stressed plants of both species in the light fully recovered. In the shade, only A_{sat} of *Hepatica* recovered but *Asarum* did not. The amount of NSC, which was lower in the shade than in the light and increased with the drought intensity may have contributed to the recovery. Measurements of hydraulic conductances indicated a higher proportion of conductive xylem in plants grown in shade than in the light, in both species. To sum up, herbs in the shade were less exposed to and less affected by drought. On the other hand, light helped the plants of *Asarum* to recover from the severe water stress.

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Session 7-P15 - Xylem structure and function

Vessel diameter corresponds to vessel length in relation to water transport and xylem function

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Plants rely on their vessels for water transport, which is an essential element for their survival. However, limited research has been performed on vessel length, despite the influence vessel length along with vessel diameter can have on plant water transport. The goal of this study is to compare vessel lengths and diameters in branches of woody angiosperms from Central Europe across species, also to examine whether vessel length depends on vessel diameter within any stem of each species selected. A total of 11 species was studied, including ring-porous and diffuse-porous species. Five stems were measured for each of the 11 species studied. The highest possible level of standardization was prioritized. Comparison of mean vessel lengths were conducted using the pneumatic method, and maximum vessel lengths were measured through air injection using a syringe. Vessel diameters were evaluated based on light microscopy. We hypothesized that ring-porous species would have longer and thicker vessels than diffuse-porous species, and there would be an association between vessel length and vessel diameter. Our results demonstrate that there is interspecific heterogeneity in vessel lengths and diameters. The lengths and diameters of ring-porous species are substantially larger than those of diffuse-porous species. We concluded that the pneumatic approach allows relatively fast and accurate measurements of vessel lengths. Also, understanding the scaling between vessel diameter and length contributes to our understanding of structure-functional aspects of xylem water transport. The significance of this study is to substantiate previous infusion methods and theoretical models when attaining vessel length data.

Session 7-P17 - Xylem structure and function

Drought impact on shoot hydraulic conductance and anatomical elements of sessile oak coppice and high forest

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10 branch (stem) samples were taken from sessile oak (*Quercus petraea* (Matt.) Liebl.) coppice, seedlings and mature trees during the vegetation season of 2018. We measured and compared actual (K_a) and maximal (K_{max}) stem hydraulic conductivity and used them to calculate percent loss of conductivity (PLC). Those variables were then linked to predawn and noon leaf water potential (ψ_l) measurements to determine the level of drought stress. The same stem segments were sectioned using a microtome and stained with a solution of safranin and alcian blue. Vessel lumen area (A_{lum}), average maximum (d_{max}) and minimum (d_{min}) vessel diameter of each cross-section; number of vessels (N_{trach}), area (A_r) and width (W_r) of the last annual ring in a cross-section were analyzed using ImageJ.

The highest water stress at noon (midday ψ_l) was again in seedlings -4.2 ± 0.3 MPa, and -3.7 ± 0.1 MPa and 3.4 ± 0.1 MPa in mature trees and in the coppice, respectively. No significant differences were found between the forest management systems in PLC, K_a and K_{max} . However, in mature trees, the PLC was increasing with increasing drought level and during the season (from 71.65 ± 6.14 % in July to 87.63 ± 3.83 % in September). The further aim is to assess how the different growth rates of various forest management systems affect wood properties throughout anatomical elements, which are crucial for hydraulic safety.

The study was supported by Ministry of Education, Youth and Sports of the Czech Republic (Grant INTER-TRANSFER LTT20017).

Session 8-P1 - Ecosystem water fluxes

Differing hydraulic strategies and radial sap flow patterns are determined by xylem anatomy and stem water storage in four co-occurring temperate tree species

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Knowledge of hydraulic strategies is essential to understand the response of forest ecosystems to changing environmental conditions. Therefore, we investigated the water use strategies of four temperate tree species (*Abies alba*, *Fagus sylvatica*, *Picea abies*, *Quercus petraea*) and assessed the influence of environmental drivers on hydraulic strategies. In 2021, we conducted a study in a mature forest measuring sap flow (SF), stem radial variation, water potentials and water stable isotope ratios to identify responses of tree water status on varying meteorological conditions. Vapor pressure deficit (VPD) and photosynthetic active radiation (PAR) were the most important drivers of SF under moist conditions. *A. alba* was the species with the most conservative water use strategy, whereas *F. sylvatica* had the highest responsiveness and loosest stomatal control of SF to environmental drivers. We further observed a strong regulation of sap flow rates for *Q. petraea* with declining stem water content in the outer xylem, whilst SF in the inner xylem remained unaffected and even exceeded SF in the outer xylem during peak transpiration. All species showed a pronounced hysteresis in their diurnal SF-VPD/PAR relationship and high contributions of nocturnal SF to overall water consumption. Towards the end of the vegetation period considerable rates of reverse flow occurred in conifers most likely related to phloem sugar dynamics. In conclusion, we found different hydraulic strategies in our four tree species associated with xylem anatomy, stomatal control, and stem water storage.

Session 8-P2 - Ecosystem water fluxes

Recurring drought stress with concurrent leaf area changes alters the radial profile of xylem sap flow density in mature spruce

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The past decade in Central Europe revealed the devastating consequences of severe and repeated drought/heat events on forest ecosystems. Nevertheless, responses of the water balance of mature trees and forest stands to such repeated drought events and subsequent recovery are still scarce. In the Kranzberg roof experiment (KROOF), precipitation throughfall was excluded during five consecutive growing seasons via retractable roofs in a mature beech-spruce forest, resulting in pre-dawn leaf water potentials as low as -1.8 MPa. The drought-induced reduction of stomatal conductance led to a reduction of sap flow density (u_{daily}) in the outer part of the xylem by up to 80% and 40% in spruce and beech, respectively. Nevertheless, repeated throughfall exclusion did not affect the radial xylem sap flow profile in beech. In spruce, however, u_{daily} was strongly reduced across the profile under repeated drought, altering the profile from a linear to a logarithmic regression. While u_{daily} in the outer part of the xylem increased again after drought release to more than 90% of control within 2 years, reductions in the radial profile were still prominent after two years of drought release. This reduction of u_{daily} along the radial profile was accompanied by a strong reduction of the leaf area (LA) by about 50% in spruce, but without changes in the sapwood area (SA), decreasing the LA/SA ratio. **Therefore, water use in formerly drought-stressed spruce was still reduced by over 30% after drought release leading to an overestimation of water use via standard profiles.**

Session 8-P3 - Ecosystem water fluxes

Intra- and interspecific competition effects on tree water use and tree structure

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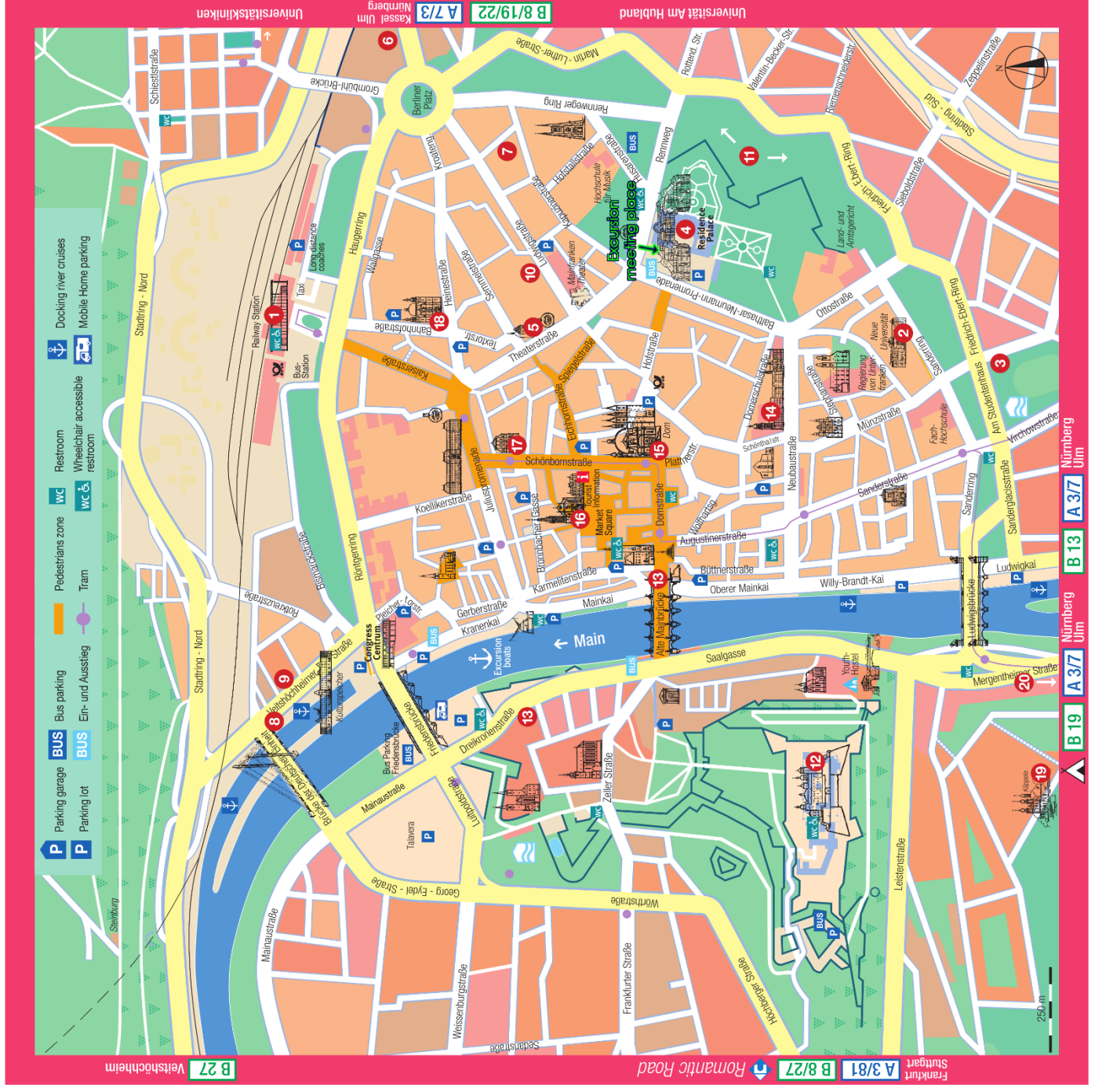
Changes in future climate conditions will affect forest ecosystems. Understanding the linkages and interactions between water use strategies, water storage and competition effects can thereby provide valuable knowledge about drought resilience of different tree stands. To this end, we assessed water fluxes at high temporal and spatial resolution in a forest in South-West Germany. Measurements were conducted in pure and mixed tree stands with two temperate tree species, European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*). Sensors recorded sap flow and stem water content combined with continuous measurements of water stable isotope ratios by recently developed membrane-based in-situ isotope assessment. Additionally, a terrestrial lidar scan contributed tree structure data. Our central hypothesis is that species identity and water competition between tree species is a major driver for ecohydrological flux dynamics. Spruce showed lower sap flux density in mixed stands compared to pure stands while the opposite effect was observed with beech. Beech depleted its stem water content more during the day compared to spruce. Water isotopy of beech in pure stands showed the fastest reaction to precipitation signatures indicating a direct uptake of throughfall and stemflow water. Overall, results showed above ground competition effects by changes in crown density distribution including differences in water uptake and stem water management.



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Map of Würzburg



5. Xylem
International Meeting
XIM5 | Würzburg
19 - 21 September
2022

- 1 Main train station
- 2 Conference venue
- 3 Canteen 'Burse'
- 4 Würzburg Residence Palace
- 5 Bürgerspital wine estate

HOTELS

- 6 GHOTEL
- 7 Dorint Hotel
- 8 Ibis Hotel
- 9 B&B Hotel
- 10 Hotel Amberger

SIGHTSEEING

- 11 Ringpark
- 12 Fortress Marienberg
- 13 Alte Mainbrücke (old bridge)
- 14 Old University
- 15 Cathedral of St. Kilian
- 16 Church Marienkoppele
- 17 Church Augustinerkirche
- 18 Church Siff Haug
- 19 Church Kärpele
- 20 Botanical Garden