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Editorial

Jan Čermák's lifetime contribution to tree water relations

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Overview of life and academic career

One of the giants in Czechoslovakia – now the Czech Republic – in plant water relations, Professor Jan Čermák, passed away on December 23, 2021, in Brno, Czech Republic. Following in the footsteps of earlier noted Czech physiological ecologists – Jiří Čatský, Pavol Eliáš, Josef Huzulák, Zdeněk Šesták and Bohdan Slavík – Jan Čermák carved a reputation in plant water relations. Unlike the others, Čermák collaborated globally in his research endeavors, and these collaborations spanned almost four decades.

Jan Čermák was born on July 23, 1938 in Prague, Czechoslovakia as the second son in the medical family of Doctor Václav Čermák. He grew up in Prague in an intellectually stimulating environment and his personality was strongly influenced by his years in scouting. For his entire life, he remained very fond of the capital city and of Central Bohemia. He started exploring nature as a high school student and was soon accepted in the Czech Ornithological Society, where he cooperated with the recording of observations of banded birds by the National Museum in Prague. In June 1957, he completed, with honors, high school in Říčany, a small town just southeast of Prague. Until September 1958, he worked as a forest laborer at the Jílové forest plant and two years later, in 1960, he graduated from the forest technical school in the town of Písek. He decided to enroll for Master studies in the Faculty of Forestry of the Agricultural University of Brno in 1960. Brno became his new, beloved hometown and he fully enjoyed the landscape, nature and forests of Moravia. In June 1965, he obtained a Master of Science degree with high distinction. After having completed his full-time military service in September 1966, he joined the Vlašim forestry enterprise as a forest engineer/silvicultural technician. Between 1966 and 1967, he completed two study stays, one at the Institute of Instrumental Analytical Chemistry of the Czechoslovakian Academy of Sciences in Brno and one at the Norwegian Forest Research Institute in Vollebekk. Subsequently, he became a research assistant (1967–1969) at the Institute of Forest Botany and Phytocenology, Forest Faculty of the Agricultural University of Brno.

Shortly thereafter in 1971, while he was working at the Institute of Forest Botany and Phytocenology, the rector of the same university noticed him and offered him a position at the Institute of Forest Ecology, founded as part of the large international Man and Biosphere (MAB) project. The Czech participation in this project was canceled by the new government, but the Institute somehow survived. Early in his career Čermák studied volatile compounds and liquid fractions of terpenes, secondary metabolites released by trees for their defense and communication. This subject area formed the foundation for his dissertation. However, his research interest soon turned toward the measurement of water movement through stems and roots of trees as well as to the development of instrumentation to measure these water flows. He posited that understanding water movement would provide a direct path to a tree's water status and thus a link to a tree's oleoresin status and production.

Together with Mirko Deml from the Institute of Instrumental Analytical Chemistry, Čermák invented a method for measuring water movement in tree stems and built the first simple device for measuring sap flow. He was setting up the first instruments when electrical engineer Jiri (Jura) Kučera started working with him as of 1973. Čermák progressed through the ranks to research worker (1970–1975) and independent researcher (1976–1977) while working toward his PhD. In 1977, he obtained the title of Doctor of Philosophy in the discipline of plant physiological ecology at the Agricultural University of Brno. Fortunately, he was able to defend his dissertation just before the restrictions of the late-seventies when many persons were fired because of their political views. He continued at the same university—later renamed the Mendel University of Agriculture and Forestry in Brno—as independent research specialist (1977–1984), research scientist (1985–1989), senior research scientist and leader of the tree ecophysiology research group (1990 and later).

For context, it is important to remember that 1938 to 1989 was a period of great political and social upheaval in eastern Europe. Čermák's home country experienced the occupation by Germany, the Second World War, a short period of recovery and a restoration of Czechoslovakia, and then in 1948, it became part of the communist east bloc. An attempted liberalization in the spring of 1968 was put down by a Soviet invasion of the country. These were very restrictive times. Information flow into and out of Czechoslovakia was greatly restricted and travel, especially for non-members of the Communist Party, was almost impossible. The term Iron Curtain was not a misnomer. In 1983, Čermák undertook his first international collaborative research project with Rainer Matyssek and Detlef Schulze near Bayreuth in Bavaria, West Germany. This was remarkable as Čermák was still a relatively unknown researcher toiling under strict communist rule. To his credit, Schulze recognized the great promise of the tissue heat balance (THB) sap flow instrument that Čermák developed, and was able to part the Iron Curtain to enable Čermák and Kučera to travel to Germany. This first external collaboration would lay the foundation for many more international partnerships that characterized the rest of Čermák's research career.

In 1988 in the USA, Dynamax's sap flux measuring system based around external heaters and thermocouples was introduced and rapidly dominated. Čermák and Kučera's second international collaboration began in Sweden in early 1989, before the Czech Velvet Revolution, and led to the first toe-to-toe comparison between the two methods. Thereafter, the THB method dominated in European tree water relations research. Čermák wasted no time after the opening of Czechoslovakia to the west. From 1991 to 1992, he was a Bullard fellow at Harvard Forest, Harvard University, USA. While in the USA, he attended his first international workshop meeting at Jackson Hole, Wyoming, leading to a collaborative chapter in a noted Academic Press book and to collaborations in the USA. During some successful international research campaigns, Čermák worked together with several scientists from Europe and the USA with whom he later started long-term collaborations and friendships. After his return to Brno, he became associate professor of tree ecophysiology at the Agricultural University in Brno as of 1992. On January 1, 1993, Czechoslovakia was separated in the Czech Republic and the Slovak Republic.

At a scientific conference in 1991 in Pushchino near Moscow, Čermák met Nadezhda Nadezhdina, who was measuring sap flow rates in orchards at the Institute of Irrigated Horticulture in Melitopol, Ukraine. In 1995, he invited Nadezhdina to Brno to compare calculations of data sets of water fluxes. From then onward, Čermák formed a well-functioning team with Nadezhdina and her husband Valerij Nadezhdin, with strong expertise in the measurement of water fluxes. In 1999, Čermák was appointed full professor of tree ecophysiology at the Mendel University of Brno. After having spent 37 years in the Institute of Ecology, he returned in 2008—already at retirement age—to the Institute of Forest Botany, Dendrology and Geobiocenology of the same university where he remained active in research and international collaboration until his death. He passed away in Brno on December 23, 2021 at the age of 83 years. Relatives, close friends and colleagues said a last farewell during the funeral in Brno on January 7, 2022.

During his academic career, he published over 300 scientific articles, conference papers, book chapters and research reports. Among these, 139 original, peer reviewed publications have been archived in the worldwide Web of Science database. These peer reviewed publications have received 5510 citations in total, and 15 publications were each cited more than 100 times. With a Hirsch-index of 44 Čermák became one of the most cited scientists not only of the Mendel University of Brno, but also of the Czech Republic. Čermák's outstanding academic achievements were internationally recognized in the form of his membership in national and international institutions, for example as: vice chair of the IUFRO Working Group on Whole Plant Physiology, member of the editorial board of the journal *Tree Physiology*, member of scientific councils of several research institutions and member of the National Committee of the Academy of Sciences of the Czech Republic for the Geosphere-Biosphere. He has lectured at several Czech universities as well as at approximately 50 universities abroad, including the Universities of Oxford (UK) and Harvard (USA). He was involved in many international research projects and academic collaborations, some of which are presented and discussed in the section below. He was a sought-after reviewer of more than 60 scientific journals, an opponent of 35 dissertations or habilitations, as well as the supervisor of 20 Czech graduates and doctoral students, and 30 foreign doctoral students.

During his lifetime, he received the following honors and awards: Dean's Award of the Faculty of Forestry of the

University of Applied Sciences for scientific achievements in 1978–1998; Award of the Czech Literary Fund, Section for scientific literature, Prague, 1981; Commemorative Medal of the Rector and the Academic Senate of the University of Applied Sciences Brno, 1986; Medal for Merit in Research in the field of tree physiology and long-term pedagogical activity, Mendel University of Brno, 2014. His footprint at the Faculty of Forestry and Wood Technology of Mendel University in Brno is indelibly engraved not only on the campus in Černá Pole, but also on the school forestry farm in Křtiny, where he conducted his research for many years, especially on the permanent research area in Soběšice.

Collaborations

First, it is critical to note that Čermák's research thrived with the support of two long-term co-investigators, Jiri Kučera and Nadezhda Nadezhdina, with whom several approaches to measure branch, root and stem sap flux were conceptualized and developed. Most often with these two individuals Čermák collaborated with researchers and scientists in Austria, Belgium, the Canary Islands of Spain, Germany, Italy, Portugal, Sweden and the USA where his techniques and approaches were brought to bear on interesting research problems and questions. Čermák's focus on trees spanned from the use of an 87-m tall Liebherr 550 Crane with an 85-m jib to assess the crowns of tall trees in an old-growth *Pseudotsuga menzesii*/*Tsuga heterophylla* forest in the Washington State Cascades to under the surface roots of a 60-year-old *Quercus suber* tree in a deciduous forest near Lisbon, Portugal. To all these endeavors, he brought creativity, energy and success—and last, but not least, verve for teaching. Just one prominent example here is his involvement in a summer school provided by the European Commission in 2013 as a docent and experimental supervisor of an international group of young scientists in the laurel forests of Tenerife Island (Spain). He constantly pushed the edge of what we knew about water transport and its pathways in woody plants. Noteworthy to all of them was Čermák's full and broad engagement with everyone from senior collaborators to short-term undergraduate student workers. While Čermák collaborated with dozens of scientists across the globe in his long career, we highlight four in this contribution: his work with collaborators in Germany and Sweden, which opened the proverbial 'doors to the west', and work in the Pacific Northwest, USA and Belgium, which both were long-lasting and highlighted Čermák's characteristic strengths as a scientist, a collaborator and a friend.

Examples 1 and 2: Germany (Rainer Matyssek) and Sweden (Emil Cienciala)

The German collaboration was initiated in 1983 by Detlef Schulze, Universität Bayreuth, Germany when he visited with Čermák in Brno to learn about the THB method. Together with Rainer Matyssek Čermák began first in the Rájec forest 30 km NE of Brno in a 72-year-old *Picea abies* plantation, and soon after in a 33-year-old hybrid *Larix decidua* × *L. leptolepis* forest 5 km north of Bayreuth. The focus of these measurements was on the diurnal dynamics of twig transpiration and whole–tree water flux as simultaneously assessed through gas exchange measurements and THB, respectively, enabling localization and quantification of tree-internal hydraulic capacitances (Schulze et al. 1985). Čermák and Kučera were consequently invited by Matyssek at the Swiss Federal Institute for Forest, Snow and Landscape Research in Birmensdorf, Switzerland to investigate the die-back of *Fagus sylvatica* (Čermák et al. 1993). The study elegantly demonstrated that drought, not air pollution, was the culprit. These events opened the door to the west and spoke of the power of the THB method.

The Swedish endeavor started in 1989 when Čermák and Kučera collaborated on several projects with Čermák's former MSc student Emil Cienciala and his two Swedish advisors, Jan-Erik Hällgren and Anders Lindroth—both at the Swedish University of Agricultural Sciences—who made the collaboration possible. The first project involved measuring sap flux velocities and radial velocity profiles in a *Picea abies* forest near Skogaby, Sweden (Čermák et al. 1992). Notably, this project was among the first in which THB technique was used to quantify responses in a manipulative silvicultural experiment—in this case with control, drought, irrigation, fertilization. At the time it was quite difficult to deploy multiple sap flow sensors simultaneously, so the study began with just two trees in 1989 (Cienciala et al. 1992), eventually building up to continuous sap flow measurements on five to six trees in 1990 (Cienciala et al. 1994). This was quickly followed by a project in 1991–1993 focusing on short-rotation willow. For this project the THB method was modified by Kučera and Čermák to be used on small diameter woody stems. The results were published in Lindroth et al. (1995) and several other papers. The final Swedish collaboration (1993–1998) was with the NOPEX project in Norunda, near Uppsala, Sweden, an experimental site with one of the first eddy covariance systems in Europe. Here the focus was on THB measurements in large diameter coniferous trees and scaling tree measurements to the stand. This research initially (in 1993) presented a study on individual tree sap flow variation and transpiration using 24 trees (Čermák et al. 1995) and then (in 1994 and 1995) one of the early comparisons of scaled sap flow estimates of stand transpiration with independent eddy covariance measurements (Grelle et al. 1997, Cienciala et al. 1998) and species-specific drought response (Cienciala et al. 1997).

Example 3: Pacific Northwest USA (Tom Hinckley)

Čermák's connections to the Pacific Northwest, USA and Belgium are rooted in a September 1991 workshop at the University of Wyoming/US National Park Service's Research Station on Jackson Lake, Wyoming. Čermák—who was Bullard Fellow at Harvard Forest at the time—was invited based primarily on the organizer's familiarity with his groundbreaking work developing sap flow technology. He left Wyoming as one of the authors on a chapter in Resource Physiology of Trees (Pallardy et al. 1995) and a plan to travel to Seattle with Kučera to collaborate with Tom Hinckley, Reinhart Ceulemans (Belgium) and Rick Meinzer (Hawaii) on the water relations of clonal hybrid *Populus*. The study site was Washington State University's Farm 5 Research Station, located just south of and in the floodplain of the Puyallup River. It should be noted that Čermák at that point already had an extensive background in studies of tree and forest water relations in such ecosystems (Čermák et al. 1980, 1982, 1984).

The broad objective of the *Populus* research was to evaluate the extent to which different types of canopies are self-regulating, or homeostatic, in the face of changes in atmospheric variables such as vapor pressure deficit—in other words, to determine how decoupled they are from the atmosphere. As Čermák had been doing for years, an essential element of the approach was to make concurrent measurements of vapor fluxes and associated driving forces at multiple scales of observation from single leaves to entire trees. The study took place in a clonal 18-tree block of *Populus trichocarpa* × *P. deltoides* F_1 hybrid clone 50–194. The three-month study began in late July 1992, the middle of the fourth growing season. Measurements included whole–tree sap flux measurements of six trees ranging in height from 11.0 to 15.1 m (diameter at breast height of 8.3 to 15.1 cm); branch sap flux in two upper, two middle and two lower crown proleptic branches; stomatal conductance on multiple leaves at three canopy positions; and stem and branch hydraulic conductance.

For estimates of hydraulic conductance and pathway, Čermák supervised a crew to stabilize a tree and cut the stem under water and then to supply the submerged cut surface with 0.5% acid fuchsin dye (Čermák et al. 1992). Proleptic branches from different heights on neighboring trees were covered in plastic, removed, immediately re-cut under water and treated like the stem. After allowing dye uptake for a timed period the stem was serially sectioned to independently estimate sap flux velocity, and to determine sapwood area. Ever the forester, Čermák assumed the task of tree inventorying for the clonal block. Branches were sampled to determine the vertical distribution of leaf area. The biometric and physiological measurements were used to estimate whole stand, tree and branch water flux. The analysis revealed that the large-leaved, dense canopy with high stomatal conductance was poorly coupled to the evaporative environment (omega factor = 0.66), and that within-canopy variation in stomatal conductance and leaf specific hydraulic conductivity were linked to patterns of radiation extinction (Hinckley et al. 1994).

The success of the campaign in the simple *Populus* canopy led to subsequent group efforts in naturally regenerated even-aged *Abies amabilis* stands and even more complex old-growth *Pseudotsuga menziesii*/*Tsuga heterophylla*, all on the west slope of the Washington Cascades mountain range. The campaign from the younger *Abies* stand showed how transpiration was partitioned among crown classes (74% of stand transpiration came from the largest third of trees, while less than 10% came from the smallest third of trees, Martin et al. 1997); produced an empirical model of stand level sap flow (Martin et al. 1997); and defined scaling relationships from shoot to branch and branch to tree (Hinckley et al. 1998). Analysis from the old growth *Abies* forest revealed temporal and spatial variation in coupling within the stand and illustrated how branch-level fluctuation in sap flow related to tree-level transpiration patterns (Martin et al. 2001).

In 1996, the opportunity to study the water relations of truly old and tall trees emerged with the erection of a construction crane in an old growth *Pseudotsuga menziesii*/*Tsuga heterophylla* forest (Shaw and Greene 2003). The study stand contained dominant *Pseudotsuga menziesii* trees over 450 years old and with heights ranging from 52 to 65.4 m. The study tree was 57 m tall, with a crown length of 31 m, and a diameter of 1.29 m. Measurement approaches were like the other Washington campaigns, with special modifications of the THB sensors for the very large tree diameters, and addition of an upper stem (51 m) sap flow array and stem radius logger at both locations to allow analysis of water capacitance. Important outcomes of the *Pseudotsuga* campaign included detailed analyses of capacitance in very large trees relative to existing information in smaller trees (Phillips et al. 2003, Čermák et al. 2007), and a contribution to the ongoing (at the time) dialogue in the literature regarding support for the cohesion-tension hypothesis (Bauerle et al. 1999).

Importantly, the Washington period highlighted Čermák's trait of engaging with early career scientists with the same enthusiasm as with well-established international researchers. Čermák imparted to these students an appreciation for the value of close observation of trees in their environment, the equal importance of structural and functional measurements in understanding tree and forest water flux, and an unrelenting focus on technical precision in measurement even under the most challenging field circumstances. Students from this period who worked with Čermák all noted the inspirational and perhaps intimidating impact of seeing a scientist older than their fathers operating mentally and physically at full throttle from dawn to dusk.

Example 4: Belgium (Reinhart Ceulemans)

In 1995, Ceulemans' research group at the University of Antwerp started intensively collaborating with Čermák—and soon with Nadezhdina. The collaborative nature of the research resulted from a joint interest in forest ecology and in the functional and structural aspects of temperate forests. The overall aim was to measure sap flow and scale-up to quantify stand transpiration and overall stand water loss in a Scots pine forest in Brasschaat near Antwerp. As usual, Čermák began the work by injecting dye into the stem of one of the study trees to quantify the conducting sapwood area and flow patterns and rate. As the tree was cut, Čermák attempted to lower the tree with a rope, an impossible task despite his great strength. This resulted in Čermák burning his hands as he did not want to let the rope go and allow the tree to fall. Despite this harrowing start, flow rate and conducting area were determined, and stem sap flux measurements were successfully monitored (Čermák et al. 1998). This first research campaign was the start of a long-term collaboration and friendship that lasted from 1995 until Čermák's death.

Čermák was always very open to people and made every effort to help where needed. In 1996, he wanted to help Nadezhdina and Fyodor A. Tatarinov to get international exposure and asked Ceulemans to host both scientists at the University of Antwerp for some experimental work. Results of this first one-month stay in Antwerp were two papers about leaf area and biomass of *Rhododendron ponticum* (Nadezhdina et al. 2004) and *Prunus serotina* (Urban et al. 2009), two invasive species in the Scots pine forest. Over the years, the long-term common and fruitful cooperation was intensified between the Antwerp and Brno labs. These collaborations were fruitful, resulting in 13 peer-reviewed papers covering a wide range of topics.

Annually from 1996 until 2008, Čermák and Nadezhdina—sometimes accompanied by a third Czech collaborator, student or staff member—came to the University of Antwerp for research campaigns or short-term study visits of several weeks (Nadezhdina et al. 2002). Čermák taught the combined research group all about the methods and techniques that he and Nadezhdina had developed for the measurement of sap flow of individual trees as well as of other physiological properties (Čermák et al. 1998, Janssens et al. 1999). He also showed how these techniques could be used for scaling of data from trees to stands and to watersheds. Sap flow measurements in trees were the common preferred method in water relation studies. Although Čermák and Nadezhdina worked as a harmonious research team, they applied different methodologies. Čermák was the author of the THB method, which was further improved by Kučera. Nadezhdina preferred methods with linear heating, which she had been using since her doctoral research in Ukraine. Just before moving to Čermák's lab in Brno, Nadezhdina tested a sensor configuration which later became known as the heat field deformation (HFD) sensor. Since then, Čermák and Nadezhdina often applied both methods for sap flow measurements in their projects (Chiesi et al. 2002, Čermák and Nadezhdina 2011), including experiments conducted in 1999 in the Hahn-Meither Institute in Berlin with Helmut Tributsch with whom they jointly published five papers.

Figure 1. Prof.-Ing. Jan Čermák at the Soběšice research site, Czech Republic on 31 May 2008. © Martin Čermák.

In a research project (1997–1999) with the Institute of Forestry and Game Management (Geraardsbergen, Belgium) and the University of Antwerp, Čermák focused on measuring sap flow rates of mature poplar and Scots pine trees for scaling them to the stand level with the ultimate goal to determine water consumption by planted poplar stands or Scots pine forests (Meiresonne et al. 1999, 2003, 2004). The results enabled the evaluation of the structural balance of trees and tree survival at the level of individual trees and stands (Čermák et al. 2008). When interpreting results of sap flow measurements, the team of Čermák and Nadezhdina took a 'divide and conquer' approach to data analysis. Nadezhdina focused mostly on tree-level measurements, except for the THB data which Čermák evaluated himself. Čermák generally took charge of scaling both sap flow methods to the stand level (Nadezhdina et al. 2007). This approach speeded up data processing. The joint research campaigns and mutual visits resulted in several joint scientific publications in international peer-reviewed journals (Nadezhdina et al. 2007, Verbeeck et al. 2007).

From 2003 until 2007, the collaboration between Čermák and his team with the University of Antwerp was formalized in and funded by several bilateral cooperation projects from the Ministry of the Flemish Community and the Czech Academy of Sciences. During the academic year 2005–2006, MSc student Raphael Bequet of the University of Antwerp completed a thesis on a comparative study of the sap flow of coniferous and deciduous trees with different root systems and contrasting water availability at the Soběšice forest near Brno (Figure 1). At Mendel University in Brno, the student was supervised by Čermák and Nadezhdina. It was a highly successful joint supervision that resulted in a scientific publication thanks to Čermák's persistence (Bequet et al. 2010). Čermák was generous in sharing his research network with his collaborators and students. Between 2004 and 2021, various researchers from Mendel University and from Čermák's research group frequently spent time at the University of Antwerp—including Valerij Nadezhdin, Josef Urban, Martin Čermák, Jan Gasparek, Roman Gebauer and Roman Plichta.

The Belgian–Czech collaboration was not uni-directional. Starting in 1995, Ceulemans visited Mendel University in Brno almost annually for periods up to three weeks to collaborate with Čermák and Nadezhdina. The first visit to Čermák's office/laboratory at Mendel University made a lasting impression. His office was stacked with folders, maps, books and data records around three very simple, humble desks. The office was also his laboratory. He had installed a folding bed on the entresols in the lab and had a small refrigerator so that he could stay in the lab overnight when necessary—often when he missed the last bus transport home. Čermák—with the help of Nadezhdina—and Ceulemans organized two joint international workshops on sap flow and water relations in Antwerp in 2005 and 2007. Intensive research collaborations with annual visits in both directions and joint publications lasted until 2015 (Gebauer et al. 2015, Urban et al. 2015).

Contributions to knowledge and science

Čermák was a skillful scientist and conceptualized several innovative techniques that were often rather straightforward, simple and easy to apply under field conditions (Čermák et al. 1998). He also arrived at technologies and approaches that took considerable knowledge of the structure and function of trees as well as of the underlying biochemistry and biophysics controlling form and function. He was a champion in combining multiple techniques and approaches together, such as the integration of sap flow measurements at the macro level (roots, branches, stems) with those at the micro level, and of anatomical studies at the cell/vessel level with root and shoot architecture analyses. He taught us how to integrate structural information at the tree level (crown, stem, root) with the corresponding sap flow. Čermák's research enabled the estimation of the absorption of water from different soil layers, as well as the dynamics of this process and its importance for tree survival (Meiresonne et al. 1999, 2003). Without Čermák's energetic and creative science, would we ever have thought about using the staining method for quantifying conducting sap wood, or the earth impedance method? Would we ever be so enthusiastic about root excavation by the 'air-spade' technique combined with photography and image analysis without Čermák's visionary ideas about applying these techniques to forest trees? In the face of his prodigious contributions to tree and forest water relations, it can sometimes be easy to forget that Čermák also developed methods and techniques for the determination of oleoresins/volatiles using ultra-trace organic analysis. He studied oleoresins as an indicator of the organogenesis of trees and their physiological and ecological properties (Čermák 1987). He also published on volatile substances in the atmosphere as indicators of drought stress of tree or primary attraction (Čermák and Novák 1986).

Technological contributions

- Sap flow: the tissue heat balance method (THB) was developed by Čermák (Čermák et al. 1973, Čermák et al. 1976*b*). He revolutionized the measure of water movement in tree branches and stems. The key element of Čermák's approach was to directly heat a defined space within the xylem with an electric current. The wood and sap were heated due to the flow of alternating current through the stem tissue acting as a resistor, instead of being heated by a metal resistance element in contact with the wood. Because the heated space was well defined, the heat balance equation could be used to determine convection due to sap flow without empirical coefficients. In this way, flow was determined as volume of water per unit time and thus provided a quantitative value of water movement. With this approach, no calibration was necessary. All aspects of this initial design underwent many engineering and technical modifications with the addition of Kučera to the partnership (Čermák et al. 2004, Čermák et al. 1976*a*, Kučera et al. 1977, Tatarinov et al. 2005). At present, this method is globally used in commercially available devices.
- Sap flux density: the heat field deformation method (HFD) is an alternative approach to quantify sap flow. The method is based on measurements of temperature gradients around a linear heater and quantifies the sap flux density, i.e., the volume of water per unit sapwood area per unit of time. The idea of the HFD method first appeared in 1991 with the 'sap flow index' or the symmetrical temperature difference measured below and above a heater, which was applied as 'drought indicator' for the irrigation of apple trees (Nadezhdina 1989, 1999). By including an additional asymmetrical thermocouple near the heater, the asymmetry of the heat field due to moving sap could be characterized. It has been empirically shown that the ratio of these two temperature differences is proportional to the sap flow rate. Positive results of synchronous measurements of sap flow by THB (measured by Čermák) and HFD (measured by Nadezhdina) in a *Laurus azorica* tree were included in the first publication about HFD in the Proceedings of the Fourth Sap Flow Workshop (Nadezhdina et al. 1998). In 1997, during a research stay in Antwerp Čermák assembled the first two multi-point HFD sensors, which for the first time allowed the direct detection of sap flow radial profile in a tree stem. This approach with multiple HFD sensors was technologically improved by Valerij Nadezhdin. After 1996, the HFD was widely used in all projects of the ecophysiology group of Mendel University conducted in Belgium, the Canary Islands, the Czech Republic, Germany, Italy, Norway and Portugal. The HFD has proven to be especially useful under conditions of bidirectional flows (Nadezhdina 2018). These advantages

are elegantly captured in the manuscripts by David et al. (2012, 2013).

- Stem staining: those who have worked with Čermák on any water transport project likely have seen him introduce dye into a tree's stem and from that introduction infer hydraulic flow rates and flow paths (Čermák et al. 1992). In the collaborations described previously, he emphasized the importance of this approach. He wrote a detailed, literature backed Manual for Staining (Čermák 1990; see Supplementary data available at *Tree Physiology* Online). In the list of equipment and materials specified in the manual, the last item was 'High patience and good mood!', something that Čermák brought to every endeavor. He proposed doing similar dye tracing in the old-growth *Pseudotsuga menziesii* study tree, but site regulations regarding coring ended that line of inquiry.
- Root architecture (air-spade, ground penetrating radar, earth impedance) and root function (earth impedance, HFD sap flux measurements) (Figure 2). It was clear to Čermák that the first step in understanding root function was to quantify root architecture (Hruška et al. 1999). Čermák's application of the air-spade technique produced some of his most interesting research supporting many of the emerging observations regarding the temporal and spatial patterns of hydraulic redistribution and bidirectional flow in roots (Nadezhdina et al. 2006, 2010, 2012, David et al. 2013).
- In summary, Čermák clearly saw the importance of measuring specific plant functional processes and morphological variables to address current research topics. He himself or with partners and collaborators developed new technologies or modified existing approaches to achieve trusted and parsimonious measurement values of structural and functional elements of trees and stands. During his career, he supplied relevant tools to identify early stress reactions of trees in relation to hydrological variables (Čermák et al. 1993, Janssens et al. 1999). This is of considerable value for studies on the effects of global climatic change on terrestrial vegetation.

Figure 2. Jan Cermák (1938–2021) under the root system of a 60-year-old *Quercus suber* tree at the Lezirias site, Portugal in 2009. © Teresa Soares David.

Scientific methods and approaches

- Čermák never forgot the intimate connections between tree and forest structure and function. Accordingly, an important element of Čermák's approach was using stand and tree inventory and structural measurements to produce detailed information on stand structure, composition and leaf area distribution. Excellent examples of such descriptions are found in research carried out near Brno (Čermák 1989, Èermák [sic] Čermák 1998) and in the first paper in a series describing the structure and function of the laurel forest type of the Agua Garcia mountains of Tenerife (Morales et al. 1996*a*). Similar notable publications focused on the three-dimensional distribution of leaf area of individual trees (Morales et al. 1996*b*) or all the aboveground tissues of a very large tree for an old-growth Douglas-fir tree (Čermák et al. 2007). These structural details are then used to interpret functional processes such as transpiration, water storage and water transport.
- Čermák was keenly aware that it was possible to take certain morphological variables and express them in such a way that they would better reflect function. Perhaps his paper on solar equivalent leaf area best captures this approach (Čermák 1989). Čermák explored the use of sapwood cross-sectional area in very different species as a morphological tool for scaling up the transpiration data between trees and forest stands (Čermák and Nadezhdina 1998). Indeed, for one species, such an approach was robust. However, for the other species, knowing the pattern of sap flow rate was a more reliable indicator (Nadezhdina et al. 2002). Such a pattern can be elucidated with different thermal approaches or through the dye staining approach that he championed.
- Čermák attempted to find approaches where the structure of root systems of trees and forests might be similarly unraveled. He teamed with individuals using the air-spade, ground penetrating radar, and the earth impedance methods to dimensionally diagram the distribution of coarse and fine roots and then to describe their roles in water absorption and movement (Čermák et al. 2006, 2008, Butler et al. 2010, David et al. 2013). This approach was taken to the whole stand level in a study of Scots pine (Urban et al. 2015).
- Integration of tissue-level water relations, with foci on uptake, transport, storage and loss, and then scaling this information for whole trees and stands. Čermák critically explored, analyzed and described the hydraulic architecture of individual trees, including leaf area and its distribution, stem and branch hydraulic architecture, root distribution (Čermák et al. 1998, 2008) and tissue storage of water (Phillips et al. 2003, Čermák et al. 2007). He also paved the road for quantifying the contributions of sap flow rate through each of these compartments and for scaling them from the individual tree to the stand level (Verbeeck et al. 2007).

Personality and conclusion

Čermák's research was groundbreaking and his legacy is impactful as he was the first to apply direct measurements of stem water flow for the estimation of water consumption, the water balance, growth and water economy of forest stands and of orchards. He had a broad interest and studied the impact of environmental stresses, such as drought, hypoxia on root water uptake patterns and whole tree water-use. From this approach, he derived proposed patterns of stress resistance and avoidance, thus documenting tree and stand vitality (Bequet et al. 2010). He applied his results in a wider ecological context to analyze the dynamics of individual tree species in mixed stands—including aspects of stability, resilience and competition. He looked at the organism holistically, from roots to leaves and his studies addressed which techniques and approaches would provide him the most trusted information about the state of water. As necessary, he would readily go from the organism to the organ, the tissue or the cellular level to understand and interpret his measurements. He was constantly moving back and forth between structure and function driven by his passion for trees and forests. His silvicultural background made him an excellent inventory person: from foliage on a twig, foliage and twigs in a crown, trees and their sizes in a stand. It was fun to watch how he thought as he was doing his work, rarely alone, often with students and collaborators, perhaps most often with Kučera and then with Nadezhdina.

Last, but not least, Jan Čermák was a famous scientist, but more importantly a very kind person with a generous soul. His passion, his curiosity, and his work ethic were contagious. Those of us, young and old, who knew him well witnessed that he was always optimistic, scientifically fully immersed and open hearted. He is greatly missed by all of us.

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Conflict of interest

None declared.

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