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Hydraulic Efficiency and Safety of Xylem Sap Flow in Relation to Water Stress in Woody Plants

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Additional information is available at the end of the chapter

1. Introduction

Trees as long-living organisms can be looked as the archives of ecological events recorded in the annual rings of wood. These can play an important role in studying and reconstruction of climate variation. The ability of a tree genotype to adjust the phenotype over the life of a tree is a consequence of short-term to long-term physiological responses to environmental changes, the ability which can be used to link environment with wood structure. The anatomical features of tree rings such as conduits size and density, cell wall thickness and the share of different tissues are sources of information on global environmental changes throughout the last millennium and on the strategies of species' responses to the evaluation of the impact of predicted climate change on vegetation dynamics.

The aim of this chapter is to present the up to date knowledge about the changes in woody plant hydraulics in response to water stress. The understanding of drought impact on plant water conducting systems structure and functioning and their possible adjustments becomes especially essential in respect to climate change projections for Central Europe predicting lower summer precipitation combined with prolonged drought periods. The issue of structural basis for water flow in wood of woody plants and the methods of its measurement and assessment are presented and the adjustments to water stress in short- and long-time scale as well as at different levels of woody plant organizations discussed.

2. Structural basis for woody plants hydraulics

Wood anatomy can be studied in the view of different disciplines e.g. technical applications, tree pathology, ecology, dendrochronology but also in terms of hydraulics as a specific hydrosystem based on cells with lumina filled with water.

In perennial vascular plants the transport of water is to great extent determined by the hydraulic architecture. This term describes the xylem network within the plant and its variations with wood type, plant age and growth form (e.g. liana, shrub vs. tree) [1]. The xylem network integrates all main parts of the plant's body, i.e. roots, branches and leaves. It means that any root in this system is more or less directly connected with any branch and not with a single one. Moreover, the xylem network is redundant in two meanings: at a given level of the stem several xylem element are present in parallel and they develop lateral contacts with other tracks of vessels or tracheids.

The xylem network is mainly represented by tracheary elements (conduits) that arise from vascular cambium periodically or continuously. Mature tracheary elements are dead cells with lignified walls. The lignin makes the xylem cells strong and prevents them from collapsing. Moreover, due to lignification the cell walls are impermeable and in effect waterproof.

The tracheids, conducting elements in conifers and ferns wood, are elongated cells with tapering ends (Figure 1A). The water moves from one tracheid to another *via* bordered pits located mainly on their end walls. The pit is an "unlignified gap" within secondary cell wall while primary wall and middle lamellae are present but structurally and chemically modified to thin membrane, through which water flows from tracheid to tracheid. In conifers, bordered pits appear only on the radial walls of tracheids except in the late wood where can also occur in tangential walls.
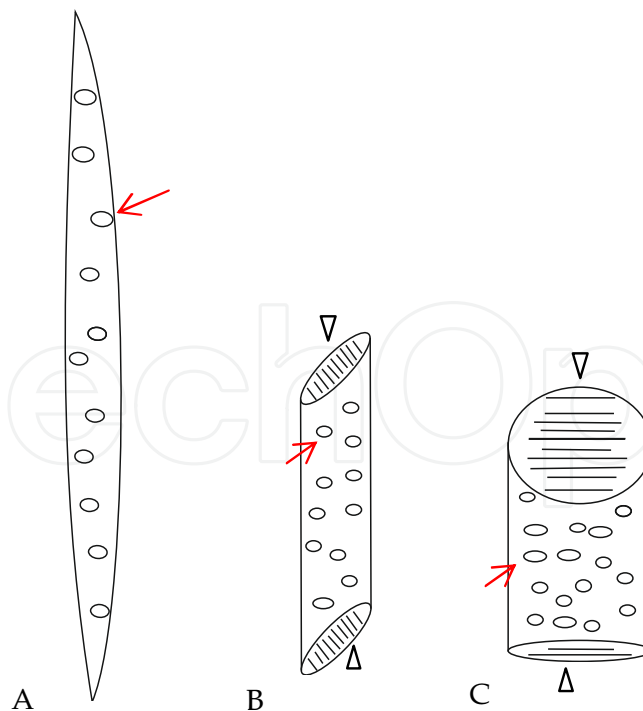

Figure 1. Schematic drawing of tracheary elements: A - tracheid, B -vessel member of late wood and C - vessel member of early wood. The bordered pits on the lateral walls of the tracheary elements are marked by arrows. Arrowheads depict perforation plates at the ends of vessel members.

Vessels, evolutionary younger in comparison to tracheids, are chief water-conducting elements in angiosperms xylem (Figure 1 B and C). They consist of the series of single cells, called vessel members. The vessel members are in general shorter than tracheids but with diameters usually larger. During the differentiation phase the end walls between two vessels members are hydrolised partly or completely and gap or gaps are formed in their end walls, thereafter called the perforation plates. The perforation plate facilitates water movement in the xylem. Vessels can be visualized as vertically aligned tubes or "pipes" made up of many cells with lignified walls that transport liquids in xylem. The vessels sidewalls have bordered pits to allow lateral movement of water.

In angiosperms two main types of wood patterns are recognized based on vessels diameter and distribution within annual ring (Figure 2). There are ring porous (Figure 2C) and diffuse – porous wood (Figure 2D). In the ring porous wood the vessels of earlywood are distinctly larger than those in the latewood of the previous and of the same growth ring, and they form a well-defined zone. In this type of wood the transition to the latewood within the same growth ring is abrupt. The diffuse-porous wood has vessels with more or less the same diameter throughout the growth ring.

In diffuse-porous species and in conifers all conduits within annual increments are responsible for water transport. In ring-porous trees water is transported mainly by vessels of earlywood whereas late wood vessels rather store water.

Generally, there is a continuous increase in the size of tracheary elements from leaves to roots. The increase concerns both tracheids length and diameter as one proceeds from branches to trunk and down into the roots. Similarly a gradual increase is found in vessel diameter and vessel length from twigs, down along the shoot and extending into the roots. The basipetal increase in vessel diameter is associated with decrease in vessel density, defined as a number of vessels per unit of cross-sectional area. The increase in conduit size can also be observed on transverse sections in a stem or a branch of a tree. The increase proceeds outward from the inner growth (Figure 3).

Tracheids and vessel members are dead cells, therefore the mechanism of water transport is based mainly on purely physical forces. Water moves spontaneously through the tracheary elements only from places of higher water potential [ψ] to places of lower water potential, i.e. along a decreasing ψ gradient (Figure 4).

In 1895, two Irish plant physiologists H. H. Dixon and J. Joly [2] proposed the cohesion-tension theory that water is pulled up the plant by tension gradient created by transpirational water lost from the leaf surface [3-5]. Although this theory is widely accepted, the alternative explanations of the mechanism of water transport are postulated. One of them is multiforce theory [6] according to which the tension gradient is supported by forces such as tissue pressure [7], or gradients in chemical activity of water [8] and absorption of water from the atmosphere adds to transpirational water uptake [9].

The basic pulling force resulting from transpiration process implies that the water in xylem is in a metastable state and thus vulnerable to cavitation that is the phase change from water to
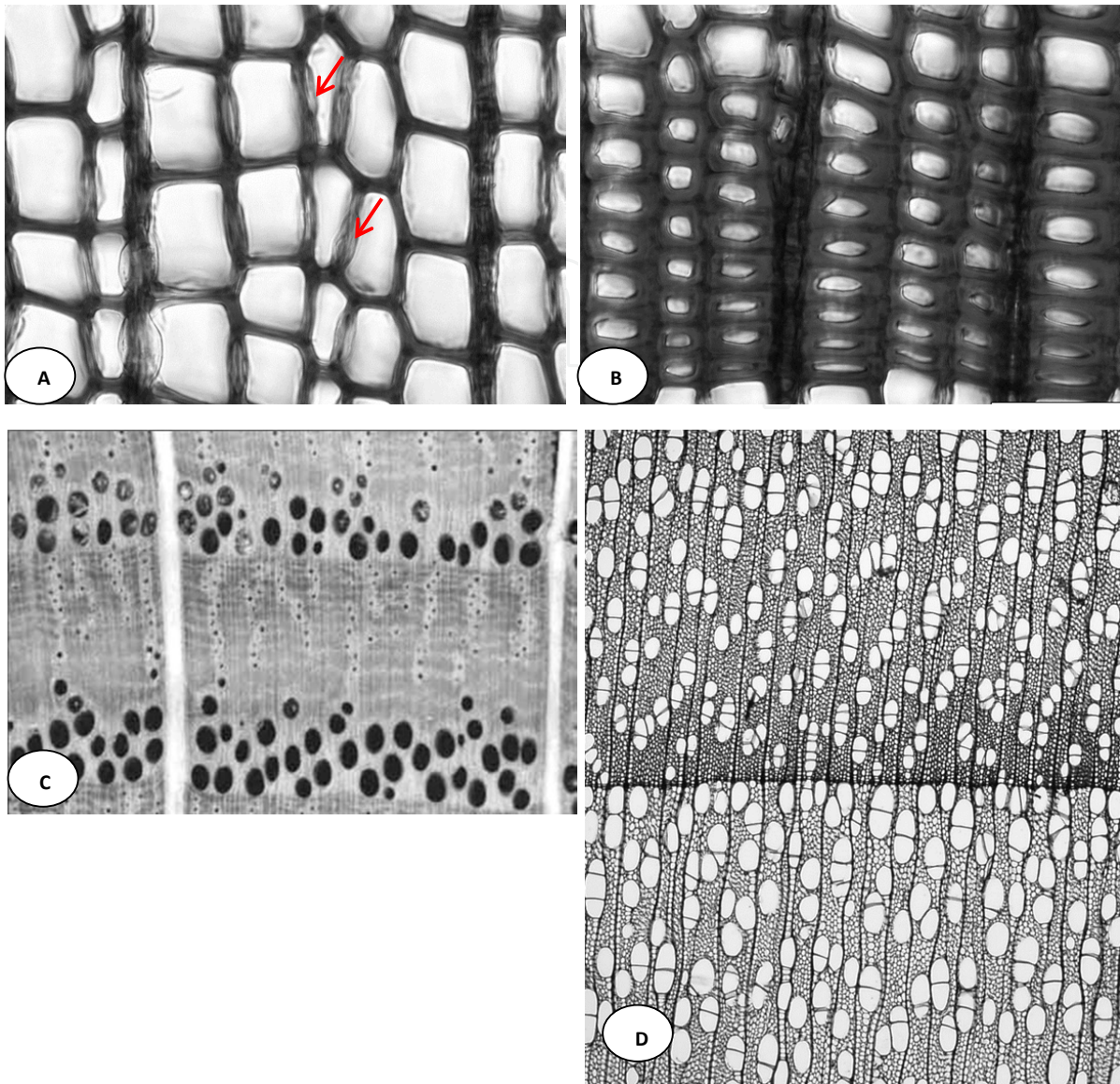
Figure 2. Microscopic cross sections of Scots pine (*Pinus sylvestris* L.) (A, B), pedunculate oak (*Quercus robur* L.) (C) and silver birch (*Betula pendula* Roth) (D) stem wood. Cross sections of: A - earlywood of pine tree (*Pinus sylvestris* L.) (x400). Tracheids with large diameter and thin cell walls are visible. The bordered pits on the radial cell walls are marked by arrows. Earlywood is mainly responsible for water transport in coniferous wood; B - latewood of pine tree (x400). Tracheids with smaller diameter and thicker cell walls are visible. The tracheids of latewood take on much of the plant support task; C - ring-porous wood of oak tree (*Quercus robur* L.) (x160). Large earlywood vessels are visible as a ring close to boundary of the annual increment; D - the diffuse-porous wood with vessels almost the same in diameter within entire growth ring (x200).

vapour. When the initially small bubble expands, blocking the ascent of water, the tracheary elements could be embolized [10]. The variety of tracheary elements in hydrosystem leads to differences in vulnerability to cavitation. More vulnerable to cavitation are vessel members than tracheids because of generally larger diameter. Therefore in vascular plants the conduction of water is a matter of compromises between safety and efficiency.
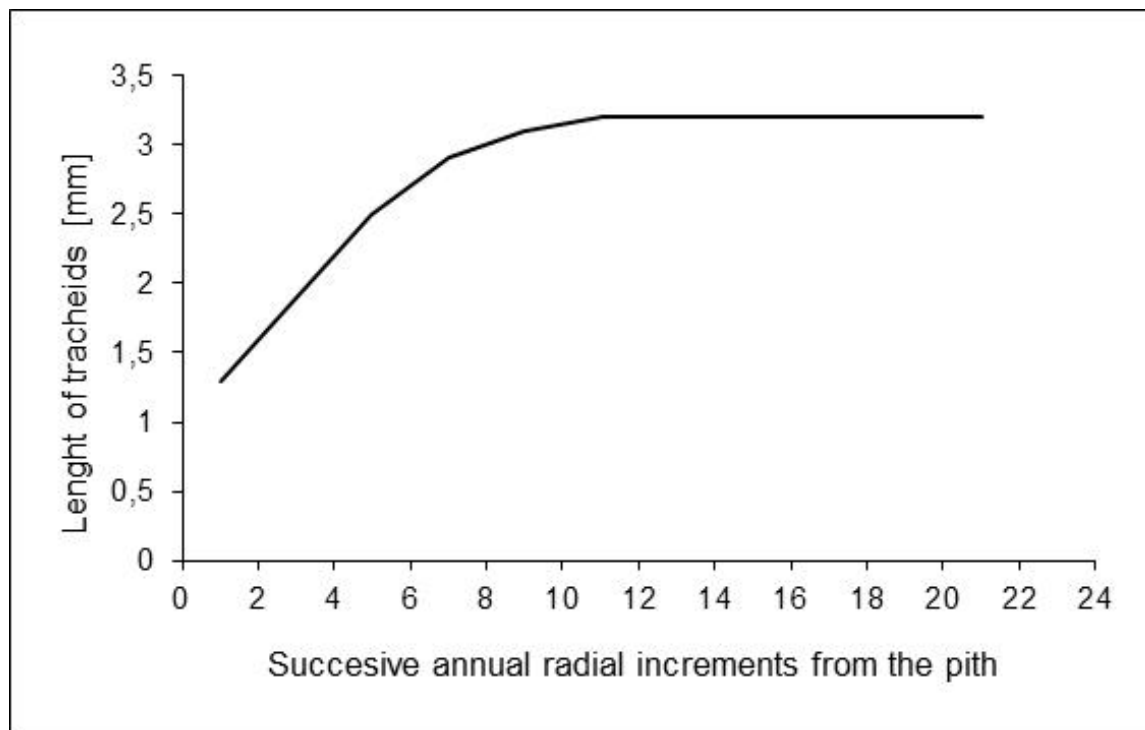
Figure 3. Variation of the tracheids length with age as the function of the distance from the pith in wood of pine tree [106, modified].

3. Measurement methods and estimators of hydraulic conductivity in plants

Our understanding of hydraulic conductivity in wood, similarly as hydraulic conductivity in soil, is based on Darcy's law that demonstrates the proportionality of water flux to hydraulic gradient and describes the effectiveness of the driving force behind the water movement. The law was formulated by Henry Darcy (1859) based on the results of experiments on the flow of water through beds of sand, thus describes the flow of a fluid through a porous medium. Darcy's law is analogous to Fourier's law in the field of heat conduction, Ohm's law in the field of electrical networks, or Fick's law in diffusion theory.

The soil and vascular plants are similar hydraulically [11], thus same physical law may be applied to describe soil and plants hydraulics. For the theoretical calculation of the volume of sap flow in the plant conducting elements the Hagen–Poiseuille equation (published in 1840) is applied, which is a special case of the Darcy-Weisbach formula. The assumptions of the equation are that the fluid is viscous and incompressible; the flow is laminar through a pipe of constant circular cross-section that is substantially longer than its diameter; and there is no acceleration of fluid in the pipe. The equation is also known as the Hagen–Poiseuille law, Poiseuille law and Poiseuille equation.

The flow of water through the tracheary element is usually compared with flow *via* smooth-walled capillary of circular transverse section. The rate of flow through such a capillary is
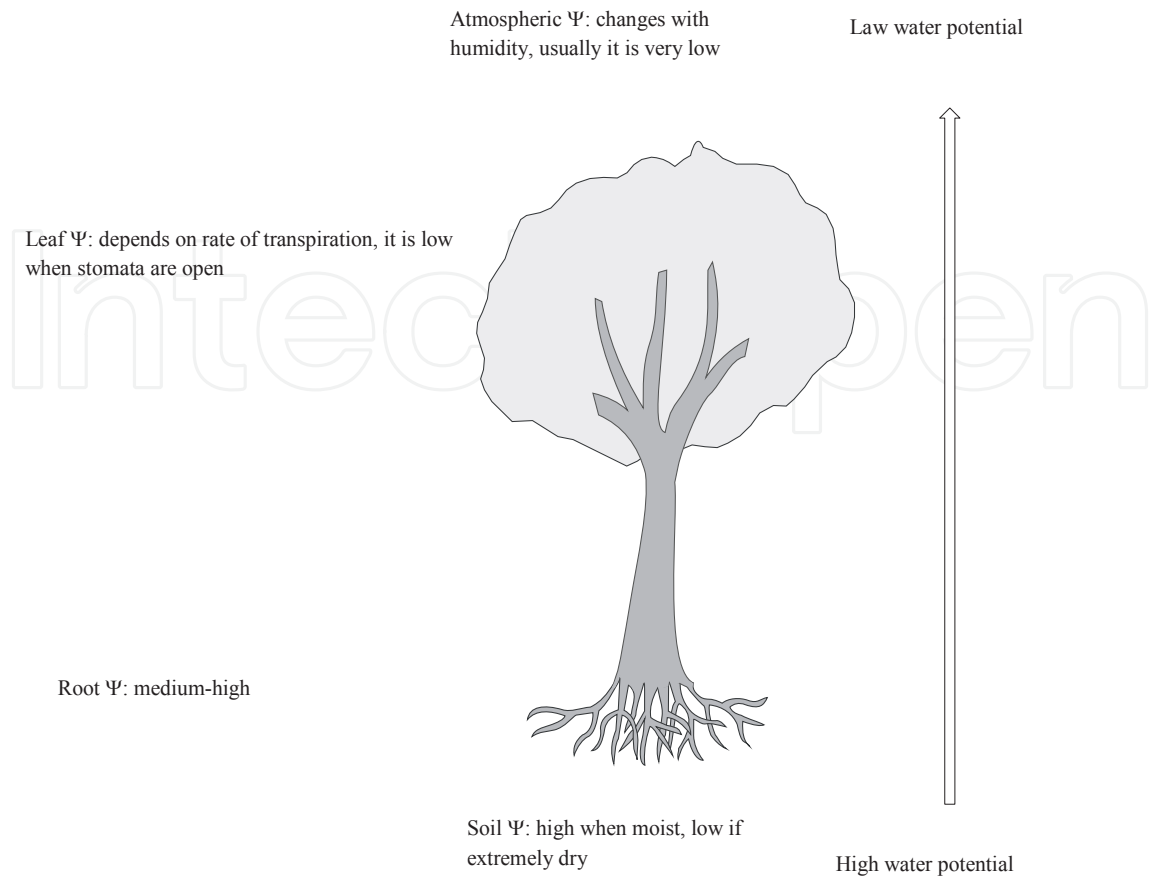
Figure 4. Scheme of water transport in Soil-Plant-Atmosphere Continuum (SPAC).

expressed in the light of Hagen-Poiseuille law to be proportional to the applied pressure gradient and the hydraulic conductivity and is written as follows [12]:

$$\frac{dv}{dt} = K_{capillary} \frac{\Delta P}{\Delta l} \tag{1}$$

where dV/dt is the rate of flow, $\Delta P/\Delta l$ is applied pressure gradient and $K_{capillary}$ is hydraulic conductivity.

Hydraulic conductivity (K) is the constant that defines the proportionate relationship of flux to hydraulic gradient and in accordance with Hagen- Poiseuille formula could be recorded as follows:

$$K_{capillary} = \frac{\rho r^4}{8\eta} \tag{2}$$

where ϱ is density of water, η the water viscosity coefficient, r the radius of the capillary.

In case of wood many conducts (capillaries) of different diameters transport water in parallel as seen in the transverse section of stems, branches or roots and thus the K_h coefficient in Hagen-Poiseuille formula is written as follows:

$$K_h = \left(\frac{\pi \rho}{128 \eta}\right) \sum_{i=1}^{n} \left(d_i^4\right)$$
(3)

Considering ρ constant at given temperature and η negligible in case of xylem sap, means that at least for theoretical considerations the hydraulic conductivity depends mainly on the diameter of tracheary elements being proportional to the fourth power of the capillary inside diameter or radius.

One of the problems in investigations focused on the vulnerability of xylem hydraulic conductivity failure and especially on the relationship between vulnerability to cavitation and vessel diameter is to find some kind of measure of average vessel diameter and vulnerability. The problem of appropriate measure of diameter arises also when comparison among taxa is in the scope of studies. As the Hagen-Poiseuille law tells, the hydraulic conductivity increases with the fourth power of conduit radius or diameter and thus wide vessels contribute dispro-portionally to the stem hydraulic conductivity, which was show e.g. for *Gnetum microcarpum* [13]. One of the ways to calculate the mean diameter is to measure 200-400 conduit diameters (D) at random and rank them from largest to smallest value after rising to the fourth power [12]. The D^4 values are summed for all conduits and then summed again until reaching 95% of the total stem conductance. The mean diameter D_{95} is calculated for number of conduits responsible for about 95% of the total stem conductance.

The mean hydraulic diameter is another estimator, based on the artificial methods of hydraulically weighting diameters distributions [12]. Mean hydraulic diameter D_H defined as:

$$D_H = \left(\frac{\sum D^4}{N}\right)^{1/4}$$
(4)

where N is the number of conduits and D their measured inner diameters, gives the diameter of vessels to be if total conductivity have to be the same as for sampled stem, providing the same number of conduits.

Hydraulically weighted diameter defined as:

$$D_S = \frac{\sum D^5}{\sum D^4}$$
(5)

has been proposed by Sperry et al. [105]. It says which vessels contribute to the greatest part in water flow and is a statistic that weights large vessels. Indeed, hydraulic diameter (D_s) has been frequently used, but some authors suggest [12] that D_h, defined as $[(\sum D^4)/N]^{1/4}$ is a better estimator, which is more meaningful measure in terms of the physics of water transport.

The index of hydraulic conductivity has been proposed by Zajączkowski [14] to compare conductivities of different tress. It relays on the sum of radii raised to the fourth power, and combines two parameters: sums of fourth power of inside vessels radii and indirectly on the vessels density as first the hydraulic conductivity is calculated per limited part of ring perimeter comprising the measured vessels but then, based on the ration of this section to whole ring, recalculated for entire ring.

The principle of hydraulic conductivity measurements also arises from the Hagen-Poiseuille formula and has been proposed and empirically tested for tree shoots [15, 16]. Briefly, in case of branch, its segment of a given length has to be submitted to a water pressure difference dP. This induces a flux which is measured with suitable device. Knowing the flux, dP and the length of the sample hydraulic conductivity can be calculated. Although the method seems simple, several precautions should be taken.

Techniques that have been first developed for study of xylem hydraulics are based on the pressure chamber, xylem pressure probe and psychrometric methods. Since the 90-ties new techniques has been applied to study xylem hydraulic and these include centrifugal force methods for measuring vulnerability curves [17], freezing-stage scanning electron microscopy (cryo-SEM) [18], and magnetic resonance imaging (MRI) methods for visually assessing embolized against functional xylem vessels [19, 20]. The pressure chamber and psychrometric methods, which are chronologically older have been successfully tested against these new techniques [21, 4]. A very promising approach to the description of some special issues concerning xylem hydraulics e.g. embolism has been developed recently based on imaging techniques that use the synchrotron X-ray light source and enable monitoring of single vessels under different conditions using 2D X-ray technique [22] and 3D X-ray technique [23].

The pressure chamber is relatively quick way for estimating the water potential Ψ_w of large pieces of tissues, such as leaves and small shoots. This method was pioneered by Henry Dixon at the beginning of the twentieth century, but come into widespread use only after the instrument design was improved and its practical use demonstrated [24]. In this technique, the organ to be measured is excised from the plant and is partly sealed in a pressure chamber. Before excision, the water column in the xylem is under tension. Excision of the organ breaks the water column (i.e. its tension is relieved allowing its Ψ_p to rise to zero), water is pulled rapidly from the xylem into the surrounding living cells by osmosis. The cut surface conse-quently appears dull and dry. To make a measurement, the chamber is pressurized with compressed gas until the distribution of water between the living cells and the xylem conduits is returned to its initial, pre-excision, state. This can be detected visually by observing when the water returns to the open ends of the xylem conduits that can be seen in the cut surface. The pressure needed to bring the water back to its initial distribution is called the *balance pressure* and is readily detected by the change in the appearance of the cut surface, which becomes wet and shiny when this pressure is attained. The pressure chamber is often described as a tool to measure the tension in the xylem. However, this is only strictly true for measure-ments made on a non-transpiring leaf or shoot (for example, one that has been previously enclosed in a plastic bag). When there is no transpiration, the water potential of the leaf cells and the water potential in the xylem will come into equilibrium. The balancing pressure

measured on such a non-transpiring shoot is equal in magnitude but opposite in sign to the pressure in the xylem (Ψ_p). Because the water potential of our non-transpiring leaf is equal to the water potential of the xylem, one can calculate the water potential of the leaf by adding together Ψ_p and Ψ_s of the xylem, provided one collects a sample of xylem sap for determination of Ψ_s. Luckily Ψ_s of the xylem is usually small (> -0.1 MPa) compared to typical midday tensions in the xylem (Ψ_p of -1 to -2 MPa). Thus, correction for the Ψ_s of the xylem sap is frequently omitted. Because the pressure chamber method does not require delicate instrumentation or temperature control, it has been used extensively also under field conditions [25] and modified by investigators in relation to the aim of the study. For example Knob et al. [26] enclosed the shoot or root system in a vacuum chamber with the proximal end protruding and supplied with perfusing solution. Flow through the xylem was induced by chamber vacuum. Hydraulic conductance was determined from the slope of the flow rate versus pressure relationship. Xylem embolism was quantified from the increase in hydraulic conductance following high pressure (100 kPa) perfusion of solution through the plant. The authors provided examples of the application of the method to cavitation studies in the cold desert shrub *Artemisia tridentata.*

The pressure probe device was developed by Ernest Steudle, Ulrich Zimmermann, and their colleagues in Germany [27] for measurements of hydrostatic pressure Ψ_p in the cells of higher plants. This instrument is similar to a miniature syringe and consists of a glass microcapillary tube which is pulled to a fine point and inserted into a cell. The microcapillary is filled with silicone oil, a relatively incompressible fluid that can be readily distinguished from cell sap under a microscope. When the tip of the microcapillary is first inserted into the cell, cell sap begins to flow into the capillary because of the initial low pressure of that region. Investigators can observe such movement of sap under the microscope and counteract it by pushing on the plunger of the device, thus building up a pressure. In such fashion the boundary between the oil and the cell sap can be pushed back to the tip of the microcapillary. When the boundary is returned to the tip and is held in a constant position, the initial volume of the cell is restored and the pressure inside the cell is exactly balanced by the pressure in the capillary. This pressure is measured by a pressure sensor in the device. Thus the hydrostatic pressure of individual cells may be measured directly. This method has been used to measure Ψ_p and other parameters of water relations in cells of both excised and intact tissues of a variety of plant species [28]. The pressure probe has also been adapted to measure positive and negative values of Ψ_p in the xylem [29]. However, technical problems with cavitation limit the measurement of negative Ψ_p by this technique.

Psychrometry (gr. *psychein* means to cool) is based on the fact that the vapor pressure of water is lowered as its water potential is reduced. Psychrometers measure the water vapor pressure of a solution or plant sample, on the basis of the principle that evaporation of water from a surface cools the surface. In one of psychrometric techniques, known as *isopiestic psychrometry*, measurement is made by placing a piece of tissue sealed inside a small chamber with a temperature sensor in contact with a small droplet of a standard solution of known solute concentration (known Ψ_s and thus known Ψ_w). If the tissue has a lower water potential than that of the droplet, water evaporates from the droplet, diffuses through the air, and is absorbed by the tissue. This slight evaporation of water cools the drop. The larger the difference in water

potential between the tissue and the droplet, the higher the rate of water transfer and hence the cooler the droplet. If the standard solution has a lower water potential than that of the sample to be measured, water will diffuse from the tissue to the droplet, causing warming of the droplet. Measuring the change in temperature of the droplet for several solutions of known Ψ_w makes it possible to calculate the water potential of a solution for which the net movement of water between the droplet and the tissue would be zero signifying that the droplet and the tissue have the same water potential. Psychrometers can be used to measure the water potentials of both excised and intact plant tissue and the Ψ_s of solutions. There are many variations in psychrometric technique [3].

Ultrasonic acoustic emission (UAE) is a non- to minimally-invasive tool to measure xylem embolism in plant organs. Its is based on the fact that when a conduit embolizes, a small amount of energy is released. This energy is detectable with ultrasonic sensors. A close correspondence between UAE and percent loss of conductivity in stems and leaves of many species has been demonstrated. UAE can be used *in situ* to assess embolism in plants growing in the field or greenhouse or can be used for generating hydraulic vulnerability curves of plant organs on the lab bench. The UAE methods can also be used for the construction of hydraulic vulnerability curves of wood or woody organs (e.g., branches). Samples are attached to UAE sensors and are intermittently weighed while collecting UAE data. Measurements of relative water content in similar samples as they dry, along with water potential using screen-cage psychrometer. Once the relationship between relative water content and water potential has been established, the weights of the UAE samples can be converted into water potentials for the construction of the vulnerability curve. Acoustic emissions have been reported in the literature as proxies for embolism events [30, 31].

Nuclear magnetic resonance (NMR) imaging (or MRI – magnetic resonance imaging) proofed non-invasive, attractive method for providing spatially and temporally resolved quantitative information on water transport at different length scales (over membranes, cell to cell, and long distance) in intact plants. This technique has been applied for visually assessing embolized against functional xylem vessels [19,20].

The potential of synchrotron X-ray light source imaging was recently highlighted in studies monitoring the status of single vessels while refilling after embolisation. Kim and Lee [22] applied 2D X-ray imaging technique for *in vivo* monitoring sap dynamics in xylem conduits in rice leaves. Brodersen et al. [23] used the 3D High Resolution Computed Tomography (HRCT) for *in vivo* monitoring of embolism repair. This technique allowed visualization of water droplets exiting from vasicentric cells and entering embolized vessels of *Vitis vinifera*. The droplets expansion over time and refilling of vessels while forcing the dissolution of entrapped gases could be observed with HRCT. This method provides access to live plant tissue at a spatial and temporal resolution. Unlike NMR imaging, cryo-SEM, acoustic emissions, and other methods used to measure embolism spread and repair, HRCT provides quantitative data for individual vessels paired with a 3D visualization of refilling mechanism.

4. Interaction between plant hydraulics and water stress

4.1. Structural adaptations

The vascular plants as the elements of Soil-Plant-Atmosphere Continuum (SPAC), grow on the edge between two environments, and are subject to water stress at irregular intervals. The knowledge of the mechanism how trees can adapt their water transport system to the specific conditions of the environment is not complete. However, it is known that when the safety of water transport is studied the biometric features of tracheary elements i.e. diameter, length, density) should be considered. Studies on tracheary elements at subcellular level are carried out as well.

Considering structural adaptation of wood to environmental settings Carlquist [32] proposed the concepts of vulnerability (V) and mesomorphy (M) indices. Vulnerability means the possibility of cavitation to occur in vessels. The V index is obtained by dividing the mean vessel diameter by the number of vessels per mm^2 transection. The low V value indicates a great "redundancy" of vessels, what means high capability of withstanding water stress or freezing. The mesomorphy index is derived by multiplying the V index by mean vessel element length. The conditions that favor better stem growth are expected to result in longer vessel elements. Analyzing the wood of florulas from southwestern Australia, Carlquist [32] found positive correlations between the V and M values and the environmental water supply in the plants studied. Mesophytes were found to have low V and high M while xerophytes possessed high V and low M values. It means that wood of plants growing in extreme habitats has high densities of very narrow vessels that are considered safe hydrosystems adapted to drought conditions [33]. On the other hand, wood of plants grown in mesomorphic environments has low densities of wide vessels which are more efficient water conductors according to Hagen-Poiseuille formula. The safety of water transport is markedly decreased as a result of increase in vessel diameter and vessel length. On the other hand, the efficientcy of water conduction is substantially increased with increasing vessel diameter and length. As was mentioned above, in ideal capillaries the water transport is proportional to the fourth power of the diameter [34]. It means that at a given pressure gradient, the relative volume of water moving *via* capillaries of diameters 1, 2 and 4 are 1, 16 and 256, respectively. To emphasize how safety is linked with efficiency of water transport, a narrow vessels tree as maple is compared with wide vessel one as oak. The first tree has diffuse porous wood with vessels diameter of about 75 μm and length of 30 cm while oak is a ring porous tree with mean early wood vessel diameter of about 300 μm and length of 10 m. Because conductivity is proportional to four power of tracheary elements diameter and taking into account vessel diameter and length, the damage done (e.g. air ambolism) to one early wood vessels in the oak is 256 x 33 = 8448 times more serious than in the maple. These numbers illustrate the contrasting needs of safety and efficiency. It means that tracheids in conifers and diffuse porous woods are conductive system of greater safety (resistance to spreading of air embolisms in the water columns) while ring porous woods with large early vessels are more efficient conductors but less resistant to cavitation. Additionally, in conifers, air embolisms if occur, can be localized within individual cells whereas in dicots vessel members it can spread from one vessel member into an entire vessel.

Another structural adaptation to eventual water stress is the ability to form groupings of vessels [35]. Grouping of vessels is defined as vessels in contact, but not merely close and is regarded as a way to provide alternate conduits whereby water can be carried in the same pathways in case one or several vessels in a group are inactivated by air embolisms. Vessels' grouping occurs to various degrees in different taxa. The degree of grouping is connected to the probability of seriousness of vessel failure by air embolisms because of either drought or frost and shows relationship to the tracheids presence in the wood. Generally in those families or genera that had tracheids in addition to the vessels, vessels are not grouped. In the families or genera with fiber-tracheids or libriform fibers in addition to vessels, the vessels form groupings to a lesser or greater extent. In the last case the genera with the larger vessel groupings seemed to be from drier localities. Species with very large vessels at the beginning of growth rings (e.g. ring porous species) tend to have little grouping in the earlywood vessels but more grouping in latewood vessels. This phenomenon is held to relate to enhanced safety of latewood vessels, since earlywood vessels have little safety and the latewood is thereby the wood portion where safety mechanisms are concentrated [36].

In studies concerning water transport of trees in respect to the risk of bubble formation due to water stress in SPAC system the geometry of intervessel pits should not be neglected. According to pit area hypothesis, during periods of water stress, the vessels with smaller diameter are supposed to diminish the risk of cavitation because of their smaller pit area per vessel [37]. The correlation between the total pit membrane area and the cavitation vulnerability would be explained by the increased chance on an exceptionally large pit membrane pore which is prone to air-seeding [38]. The studies concerning structure of the bordered pits have demonstrated that pit membranes are responsible for at least 50% of the hydraulic resistance in the wood [39]. Therefore changes in the thickness and pit porosity have to significant impact on the total hydraulic resistance in the plant. The longer and wider tracheary elements and more porous pit membrane, the lower is its resistance to water flow. As a consequence the hydraulic conductivity could be substantially increased by the little increasing the cross-sectional lumen area of the conduits and the bordered pits, but increased the conduits diameter greatly decreases the safety of water flow against the cavitations [12]. Drought induced cavitations propagate by air seeding at interconduit pit membrane [40]. On the other hand, frost induced cavitations take place when xylem sap freezes and dissolved gases form air bubbles in the wider tracheary elements capture larger bubbles in the ice that are more likely to trigger cavitation during thawing.

As was mentioned above, the size of tracheary elements is subjected to change both with the age of tree and as a result of tree reaction to environmental signals, water stress including. Tree response depends on its plasticity and ability to adapt. In the literature we can find information that in response to water deficits trees resistance changes at different levels (tissue, organ and individual) and the adjustment of trees hydraulic conductance in respect to drought could realize in three independent ways. It means that trees could increase or decrease their conductance or no changes will occur in water transport [41]. The increase of the hydraulic conductance in trees means that, on the level of wood structure, the size of the tracheary elements should increase too.

The differences in xylem hydraulic architecture reflects not only size or age-related trends but also differences in the way trees adapt to environment, and can provide information about plasticity of a species under changing environmental conditions. Tulik et al. [42] studied the hydraulic conductivity expressed both as radial weighed diameter (Figure 5) and as an index of the theoretical hydraulic conductivity in declining ash trees. It seems that more prone to the decline were trees producing smaller vessels over the course of their life, which in consequence have had negative effect on the efficiency of water transport.
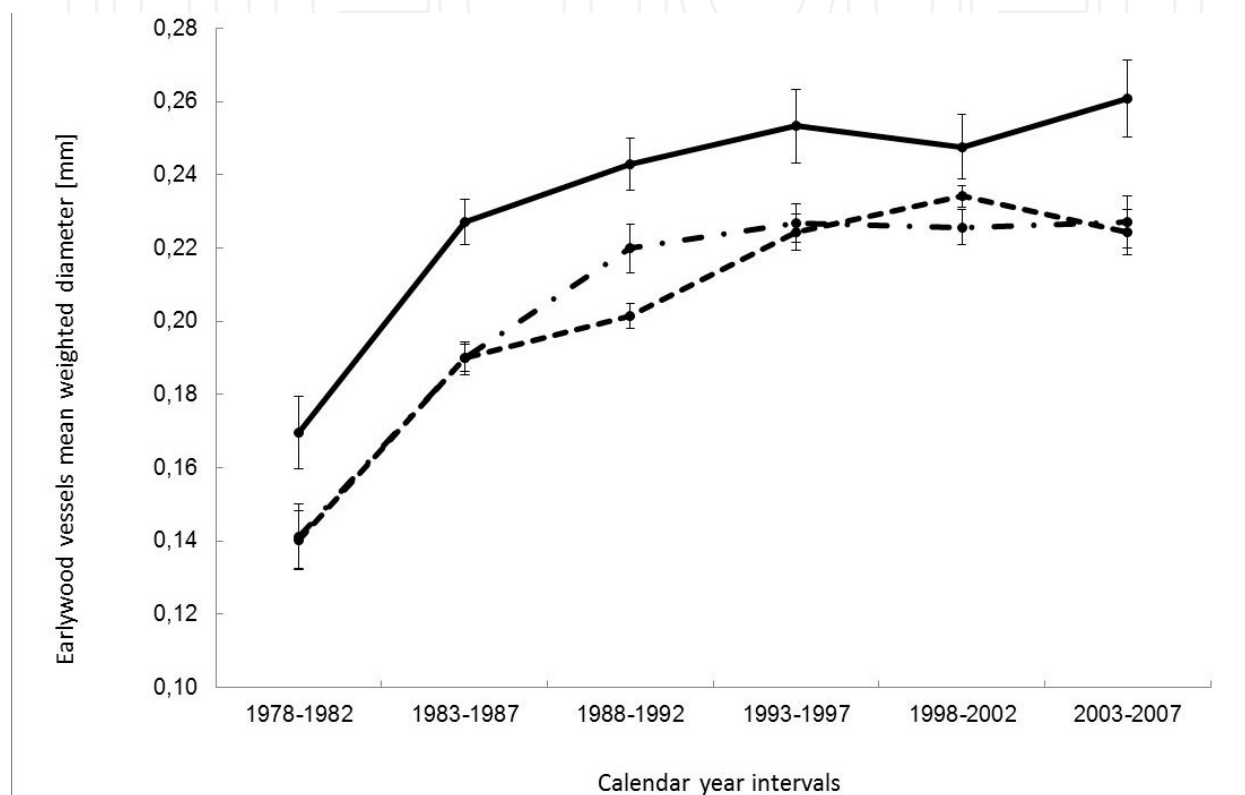

Figure 5. V ariation in earlywood vessels mean weighted diameters at breast height of European ash trees (*Fraxinus excelsior* L.), representing different health conditions at the time of sampling, over the calendar years 1978–2007. Calculations are based on at least twenty vessels diameter measurements within each annual ring and records averaged for three trees representing the group of healthy (solid line), weakened (dashed line) or dead trees (dotted-dashed line), respectively, and for 5-y time intervals. Vertical bars denote standard errors.

However, Levanič et al. [43] published somewhat contradictory results. The authors observed increased mortality of oak trees after the drainage events and concluded such results as an effect of the decrease of hydraulic conductivity by trees. Nonetheless water stress is mentioned as one among vital, possible factors responsible for the initiation and progress of the decline process of in trees.

4.2. Dysfunction due to seasonal embolism

Our understanding of the mechanism of sap ascent is based on the cohesion-tension theory ascribed to Dixon [44] which states that transpiration is the driving force pulling water from

the soil to the leaves and that the water forms continuous column under negative pressure in the xylem. Under such conditions water is in a metastable state i.e. maintained in liquid phase, while below its vapour pressure. Any break of this column drains the conduit of water, disrupts further water flow and results in dysfunction of the vascular transport pathway. A break in water column is called cavitation and occurs when a gas filled void of sufficient radius forms in water under tension. Cavitation is then the abrupt change from liquid under tension to water vapour. Within hours water is withdrawn from the conduit, vapor expands to fill the entire lumen, then air diffuses and the conduit becomes embolized (i.e. air – blocked). When water moves through the SPAC under a negative pressure, cavitation often occurs in xylem conduits [30, 45, 17, 4] Vulnerability of xylem to cavitation is an important factor in the adaptation of plants to the [46]. Cavitation of xylem has been detected in stems, leaves and roots, and appears to limit the distribution of plant species [46]. Cavitation of water columns within the xylem is deleterious for plant water relations because it results in embolism thereby reducing hydraulic conductivity [47]. Embolism can be induced by drought during summer and during winter when freeze-thaw events occur. Temperate ring porous species seem highly vulnerable to frost induced embolism [48, 49] whereas for diffuse porous the increase in embolism is gradual and requires repeated freeze-thawing events [50, 16]. Conifers practically don't suffer at all from winter embolism. These studies as well as systematic data of the degree of winter embolism [51] strongly support the traditional view that the larger the conduit, the higher vulnerability. However in case of summer embolism and resulting loss of hydraulic conductivity it seems that the vulnerability is directly determined by the diameter of the pit pores but not by the diameter of conduits.

4.3. Summer embolism and its mechanism

Trees undergo drought during summer if the soil dries, leading to a decrease of the soil water potential and increase of the hydraulic resistance at the soil-root interface. The water potential of leaves and xylem negative pressure will decrease also, promoting the development of embolism and loss of hydraulic conductivity. Reduction in xylem hydraulic conductivity can impair photosynthesis and productivity as the consequence of lower rates of carbon fixation due to stomata closure, which in turn prevents further cavitation and desiccation of leaf tissue. Under prolonged drought conditions day-by-day accumulation of embolism would finally lead to failure of xylem water transport and plant death. Thus the mechanisms to limit or avoid cavitation seem of great importance in respect to plant survival in changing environment conditions.

Among potential mechanisms of drought induced xylem cavitation the air-seeding hypothesis is favorised by experimental evidence [52] whereas in case of winter embolism the frost-thaw explanation applies [53]. The air-seeding hypothesis states that cavitation occurs when air ouside (in atmosphere or adjacent air-filled conduit) a water-filled conduit is aspired into the element through pores of the pits in the walls. Xylem sap is typically under negative pressure and hence in a metastable liquid state. It is vulnerable to cavitation, which is the abrupt phase change from metastable liquid to vapor. Cavitation is triggered by a nucleating agent, which in plants appears to be gas bubbles over a critical size. Cavitation creates a vapor bubble which

relaxes the surrounding negative sap pressure to atmospheric pressure. As long as the sap in adjacent conduits remains under negative pressure, water is pulled from the cavitated vessel and the vapor bubble expands to fill the cavitated conduit. The gas phase would expand beyond the conduit if it were no inter-connecting pits which arrest the gas-water meniscus and seal off the vapor-filled conduit. As air diffuses into the vapor from surrounding tissue, the gas pressure rises to atmospheric and the conduit is fully "embolized".

4.4. Restoration of hydraulic conductivity after cavitaion

Thinking about the mechanisms by which plants can restore hydraulic conductivity after cavitation at least two different possibilities emerge. First is to produce new xylem conduits and any plant that possesses the capacity for secondary growth can simply produce new xylem to replace the cavitated conduits. This mechanism, requiring carbon investment for growth processes, common for maintaining hydraulic conductivity in trees and shrubs, is not available to plants lacking secondary growth. Second possibility is embolism reversal through refililing with water gas-filled conduits. There is also third strategy i.e. embolism avoidance, requiring a tight control of xylem pressure, which will be discussed in the section 5. Plants adopt one or more of these strategies, which are not alternative to one another. In woody plants there is evidence for all three strategies to occur, ensuring the conductivity restoration at different time and plant body organization scale.

The disappearance of embolism means that the air should dissolve into the surrounding sap. According to the model of hydraulic conductivity recovery [54] a prerequisite for this is a positive or close to positive Ψ persisting for adequate time period. This raises the questions on how much pressure is needed to force gas into solution? for how long must this pressure operate? and how plants can generate positive pressure? For air to dissolve from a buble into liquid sap, the gas in the bubble has to be at a pressure in excess to atmospheric. Only if the difference between the gas pressure in the bubble and the pressure in the liquid surrounding the bubble is lower than the capillary pressure (resulting from surface tension), the gas will dissolve. The minimum xylem pressure (P_x) that must be exceeded for reversal of embolism to occur (P_{xr}) can be calculated on the basis of the Young–Laplace equation:

$$P_{xr} = P_{gas} - \left(\frac{2T}{r}\right) \tag{6}$$

where P_{gas} equals the sum of the partial pressure of gases filling the embolized conduit, T is the surface tension of water and r is the radius of the bubble (which can be roughly assumed to equal that of the conduit). Hence, the pressure required for spontaneous embolism dissolution is predicted to be higher for large conduits than for narrow ones. However, in contrast to the theory, intact plants can reverse embolism even when P_x in still functioning conduits is lower than P_{xr}.

The pressure required for refilling depends upon the composition of the gas contained within the embolized conduit. Immediately following a cavitation event, the embolus will mainly consist of water vapor, which has an absolute vapor pressure of 2.3 kPa at 20°C (which is –99

kPa relative to atmospheric pressure). At this moment, the pressure need only exceed this value to force these molecules back into solution. However, over time, cavitated conduits become air-filled as dissolved gases in the surrounding liquid phase come out of solution. Forcing an air bubble back into solution requires pressure greater than 100 kPa (1 atm).

Water vapor dissolves easily and refilling of cavitated conduits containing only water vapor should occur almost instantaneously once the vapor pressure of water is exceeded. In contrast, forcing air into solution is more difficult as the dissolving gas molecules locally increase their concentration in the liquid surrounding the embolus. The movement of more gas into solution is held in check by the rate at which the newly dissolved gases diffuse away from the gas–liquid boundary. Thus, the time needed to force an air-embolus into solution depends upon both the magnitude of the applied pressure and the diffusional limitations imposed by the surrounding environment [54].

It seems that plants may generate the positive pressures necessary for conduit refilling within the roots, throughout the stem, or locally, within the cavitated conduit. The mechanisms by which this occurs are fairly well understood in the case of root pressure but rather poorly understood in case of stems and local pressurization.

4.5. Generation of positive pressure in respect to refilling of cavitated conduits

The raise of the hydrostatic pressure throughout plant vascular system by actively loading solutes into root stele has been demonstrated in many species. Osmotically achieved root pressures of several hundred kPa were able to force emboli into solution or to push the air out of hydathodes or open vessel ends [55, 56]. The occurrence of this process seems to be limited to the conditions when the soil is saturated and transpiration is low and is much better documented in herbs and vines [56, 57, 58, 59] than for trees [61, 105]. Diurnal refilling owing to root pressure has been demonstrated in some crop species [56, 59], but it is uncertain whether trees employ it for daily recovery of hydraulic conductivity.

Drawing of water into stems has been demonstrated in some temperate plant species when temperatures dropped near or below freezing. Upon thawing, the positive pressure built up by this influx of water refilled embolism induced over the winter by both freezing and dehydration [16, 60]. The precise mechanism for this is not fully understood and the process occurs only in spring before leaf flush when transpiration is minimal and the soil saturated. The pressures generated throughout the stem, can co-occur with some degree of root pressure [16, 61].

Local refilling, relays on pressurization that occurs solely within an embolized conduit, and eventually could allow plants to recover conductivity during periods of active transpiration and therefore adjust to changing conditions throughout the day. This possibility is the most ecologically interesting mechanism, and there is convincing experimental evidence for the occurrence of local pressurization in woody plants.

4.6. The evidence and possible mechanism for conduit local refilling

There is growing evidence that once vessels or tracheids become embolized, at least some tree species are able to restore them to function by refilling with sap. This process has been documented with regards to reversal of winter-time embolism through spring root pressures [16, 58, 62]. Failure of this refilling can lead to crown dieback. However for a long time it was assumed that there is no recovery of embolism during drought. More recently, it was demonstrated that the refilling occurs under conditions of soil drought and in the absence of any positive bulk xylem pressure [59, 63, 64].

Hacke and Sperry [63] tested the ability of juvenile laurel (*Laurus nobilis*) and maple ash (*Acer negundo*) plants to refill embolized xylem vessels under conditions of soil drought when xylem sap pressure was substantially negative, thus seemingly violating the expected condition that pressure must rise to near atmospheric for refilling. Intact potted plants were dried to a stem water potential corresponding with approximately 80% loss of hydraulic conductivity (PLC) in shoots. Then plants were re-watered and kept at a less negative target water potential for 1–48 h. The water potential was measured continuously with stem psychrometers. Rewatered laurel held at the target water potential for 1 h showed no evidence for refilling unless water potential was within a few tenths of a MPa of zero. In contrast, re-watered laurel held for 24 and 48 h at water potentials well below zero showed a significant reduction in PLC. The recovery was highly variable, complete in some stem segments, and scarcely evident in others. Embolism repair was accompanied by a significant but moderate decrease in the osmotic potential of the bulk xylem to -67 kPa in recovering plants versus -31 kPa in controls. In contrast, embolized and re-watered maple ash plants held for 24 h at target water potential of -0 9 and -0 3 MPa showed no embolism reversal. Although for maple ash no evidence was found of novel refilling following relief of soil drought under the negative pressures tested, this species may show seasonal refilling in association with near-atmospheric or positive xylem pressures as do other members of the genus [16, 65]. Evidence for local refilling was also demonstrated for ring-porous oak (*Quercus gambelii* Nutt.) in contrast to the diffuse-porous maple (*Acer grandidentatum* Nutt.), which branches showed virtually no cavitation under investigated conditions [64]. Large earlywood vessels of 2–3-year-old oak stems cavitated extensively on a daily basis, resulting in a more than 80% reduction in hydraulic conductivity. Concurrently, oak vessels refilled on a daily basis, despite negative xylem pressure in the transpiration stream, indicating active pressurization of embolized vessels.

The precise mechanism allowing plants to refill embolised conduits under negative pressure is still not fully deciphered. The up to date known hypotheses fall into one of two categories: requiring that the embolised conduit is isolated from the transpiration stream during the refilling process and then reconnected once refilling has occurred or lacking such a requirement. There is also much more data available on the refilling in dicots than in conifers and the below presented experimental evidences concern vessels refilling first of all.

Holbrook and Zwieniecki [66] have proposed the 'pit valve' hypothesis, which requires the conduit to be isolated from the transpiration stream for local refilling. The xylem parenchyma cells adjacent to an embolized vessel secrete solutes that create an osmotic gradient for water movement into the embolized conduit. Among kinds of secreted solutes taken into consider-

ation are inorganic ions [46], sugars [67, 68, 69] proteins [70] and polysaccharides [46]. The water is prevented from draining into the neighbouring transpiration stream by persistent air pockets trapped by capillary forces in the pit chambers between the embolized and functional conduits. The pits act as valves allowing a build up of positive Ψ_{PX} in the embolized vessel. In this way, the Ψ_{PX} within the embolized conduit rises above the -2T/r limit and dissolves the gas. The valves have been shown to work in six species [71], and metabolic poisons apparently reduce the refilling activity [72]. However, for the process to be completed, the air pockets in the pit chambers must all dissolve simultaneously to re-connect the refilled vessel at positive Ψ_{PX} with the functional vessels at negative Ψ_{PX}. If an air pocket in one pit chamber dissolved before the rest, the remaining air bubbles would expand to reembolize the vessel. After some mathematical models based upon geometry and surface chemistry of bordered pits [73] at least theoretically such coordination could be achieved but how this might occur in nature remains unclear. Recently Kim and Lee [22] applied synchrotron 2D X-ray imaging technique for *in vivo* monitoring sap dynamics in xylem conduits in rice leaves and demonstrated that perforation plates of rice leaf xylem offers a substantial resistance, requiring a threshold water pressure to be exceeded before the sap can move from a refilling conduit to the next one still embolized. This observation is in accordance with the idea of the hydraulic isolation of embolized conduits [66, 71].

Other authors postulated that the driving force for water movement into hydraulically isolated conduits is an increase in tissue pressure in the cortex [7, 67, 74], which induces centripetal water flow refilling embolized conduits. An input of solutes into the refilling conduit is not predicted by this hypothesis called also the reverse osmotic hypothesis [75, 76]. According to the proposed mechanism, vessel associated cells would lower their own osmotic potential through starch-to-sugar hydrolysis. This is supposed to cause water to flow into vessel associated cells thus raising their turgor pressure. This would generate a 'tissue pressure' that would be contained within the stem by tissues external to vessel associated cell. Tissue pressure would squeeze water from other living cells and squeezed water would flow under positive pressure to the embolized conduits and refill them. A number of objections have been raised against this hypothesis, the main being that parenchyma cells would have to take up water through mass flow to raise and maintain cell turgor and at the same time deliver water through mass flow to refill conduits [46, 77].

The 'pit membrane osmosis' hypothesis [63] assumes the refilling vessel remains hydraulically connected to the transpiration stream. The living xylem contact cells are to release solutes into a cavitated vessel, thereby locally lowering Ψ_P. The solutes are to be large enough to be held back in the refilling vessel by interconduit pit membranes, which therefore act as osmotic membranes. The high solute concentration in the refilling conduit attracts water both from parenchyma cells and from the transpiration stream, generating a positive Ψ_{PX} in the embolized vessel analogous to turgor pressure in a living cell.

Convincing evidence for the role of living cells as sources of water needed for refilling was demonstrated using the potential of 3D High Resolution Computed Tomography (HRCT) for *in vivo* monitoring of embolism repair [23]. Entering of water droplets derived from vasicentric cells into embolized vessels of *Vitis vinifera*, their expansion over time and refill of vessels while

forcing the dissolution of entrapped gases, was visualized using this technique. The typical refilling time was further characterized and calculated to range between about 2 and 17 h for vessels with a diameter of 20 and 150 μm, respectively. Moreover, embolism reversal was observed at substantially negative stem water potentials ranging between −0.45 and −0.75 MPa. Droplets entered from many entry points oriented from the rays, as predicted by a refilling mechanism driven by solute pumping into vessels trough pits from adjacent parenchyma [63, 78, 79]. The authors presented an integrated model for vessel refilling that incorporates the phloem-loading and solute-driven refilling mechanisms already proposed [46, 63, 66, 69, 78, 80, 81] with amendment for successful and unsuccessful refilling.

The knowledge of embolism repair occurring while the bulk of xylem is under tension, has significantly improved during the last decade and some of the still obscure facts regarding embolism refilling have been highlighted in successive review papers e.g. [81, 82, 83]. As summarized by Nardini et al. [83] embolism repair under tension is a physiological process that requires fine coordination of (a) biochemical and morphological features of interconduit pits and perforation plates to assure hydraulic isolation of refilling conduits, (b) changes in vessel associated cells sugar metabolism to provide the necessary driving force for delivering water into embolized conduits, and (c) source-to-sink solute and water transport from phloem to the refilling conduit.

4.7. Vulnerability to embolism

Specialization during trees evolution has led to increase the dimensions of the tracheary elements. Increased diameter of tracheary elements increases the efficiency of water transport. However, on the other hand it decreases the safety of water transport, because wider conducts seem to be more vulnerable to embolism [84]. It means that trees living in unfavorable conditions of environment have usually to take a risk: the water transport lees efficient but safer or contrary, transport of water much more efficient but saddled with risk.

A plot of xylem tension causing 50% loss of hydraulic conductivity Ψ_{50} versus mean diameter D_{95} of vessels that account for 95% of the hydraulic conductance compiled for sixty species [85] demonstrates only weak correlation, as the regression accounts for only 22% of the variation. It is then not possible to predict the vulnerability to summer embolism of a species by measuring the mean conduit diameter. There is also evidence that vulnerability among trees from one genus [48] can be about as large as between diverse species of angiosperms for example. There is, however, a correlation between vulnerability curves and the drought tolerance between trees growing on sites with different water supply: the arid-sites species like *Quercus ilex* and *Q. suber* are less vulnerable than mesic-sites ones like *Q. robur* and *Q. petraea*. Seasonal change in percentage loss of hydraulic conductivity due to embolism in petioles and twigs of three European oak species shows also that several months of drought were necessary to induce a significant degree of embolism [86].

Several studies have suggested that resistance to drought-induced embolism is proportional to the ability of pits to prevent air-seeding [87, 88]. Carlquist [89] suggested that the structure of interconduit pits is a compromise between maintaining the wall strength and resistance to air entry of the inter-conduit wall without sacryfing hydraulic conductivity of the pit. Thus

inter-conduit pits act, as check valves permitting water flow between conduits but inhibiting leaking of air into the transpiration stream [44].The great variety of pit shape, size, membrane structure, border configuration, vesture presence and pit-field pattern is found in vascular plants and presumably reflect functional significance of pits. However to meet the requirements of all functions seems not possible without some trade-offs.

In the terms of the type of valve action inter-conduit pits can be rank among capillary sealing, torus-margo and vestured pits. In all cases the nonlignified pit membrane (compound primary wall) spans the pits chamber, which opens to the lumen of each conduit by an aperture. Schematic presentations of most common in dicots capillary sealing inter-conduits pits and typical for conifers torus-margo pits are on Figure 6.
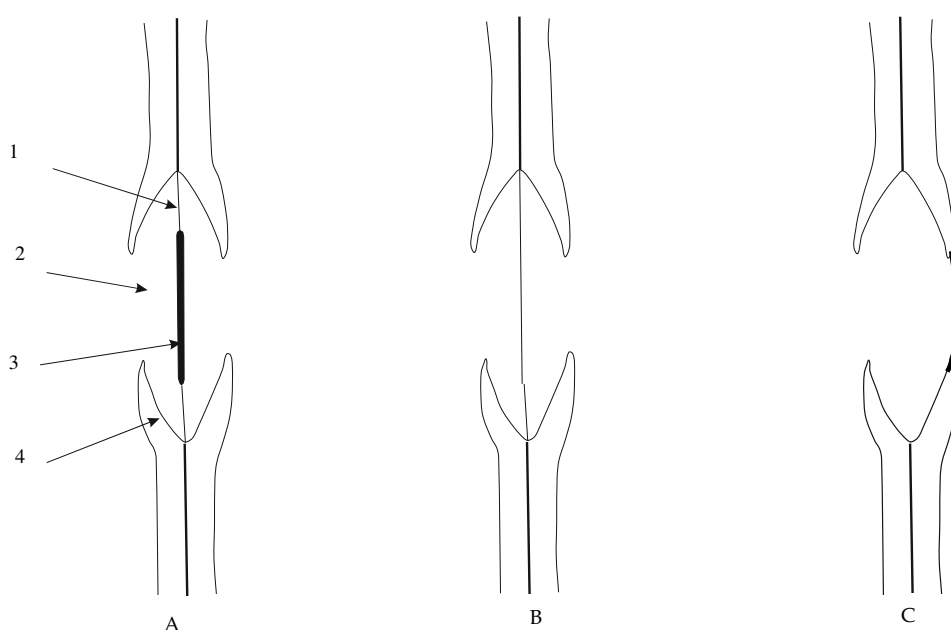

Figure 6. Schematic drawings of bordered pits in tangential view. Simplified structure of: A –bordered pit in a coniferous tree with torus in the central position allowing the water transport between tracheids, B – bordered pit in dicotyledonous tree with no torus but with uniformly small pores (not shown) in the pit membrane, C – bordered torus-margo pit when the torus closes the pit aperture. Pit elements: 1 - margo strands, 2 - pit aperture, 3 – torus, 4 – border.

Capillary sealing pits are common in angiosperms. They have uniformly small pores in their pit membranes with high air-seeding pressure, which minimizes the risk of air entry [90]. Small pores in the membrane possess however, low hydraulic conductivity. It is likely that prior to air-seeding the membrane is aspirated and distorted as the air-seeding pressure of these pores is enough to deflect the membrane to the pit border. The border of the pit supports the wall and the pit membrane against the bending force between air- and water-filled conduits. Thus pits with small or absent borders presumably indicate weak and cavitation-prone conduits but with high conductivity. Two possible ways the air seeding occurs are pointed out: irreversible plastic yielding of the membrane (creep) and reversible elastic stretching. The repeated events of membrane creep is the cause of "cavitation fatigue", which renders the conduit more prone to subsequent cavitation [91]. The investigations carried out on 27 angiosperms species with

circular bordered pits with homogenous pit membranes [92] gave the evidence for the assumption that the pit chamber itself does not weaken the wall [89] but pit aperture does. The strengthening of pitted walls is achieved by thickening of the wall but in respect to the thickness-to-span ratio which translates into higher wood density. More cavitation–resistant woods turn denser i.e. more expensive to grow than cavitations susceptible woods. It is in line with earlier observations that vessels from plants of arid habitats tend to have thicker walls [89]. More air-seed resistant pits required denser pit membranes with narrower pores, resulting in lower pit conductivity. Pores in that cases were numerous nonetheless because of nonlinear pore conductivity vs. pore diameter relationship it does not compensate smaller size.

Torus-margo pits have emerged in conifers in Jura, persist in many extant conifers, *Ginkgo*, *Ephedra* and their convergent evolution occurred in certain angiosperms. The central part of the pit membrane – torus is here substantially thicker and surrounded by a very porous margo. The air seal formation occurs through the aspiration of the torus over the pit aperture driven by capillary forces at the margo pores. Air seeding occurs eventually when the torus edge is pulled through the pit aperture [93]. Much of the membrane in this type of pits is nonconductive torus, but pores in surrounding margo can be relatively large ensuring equal or even higher total conductivity than a capillary sealing pit with more small pores.

Delzon et al. [94] examined the relationship between cavitation resistance and bordered pit structure and function in 40 coniferous species. Xylem pressure inducing 50% loss of hydraulic conductance varied widely among species, from -2.9 to -11.3 MPa. The valve effect of the pit membrane, measured as a function of margo flexibility and torus overlap, explained more variation in cavitation resistance than simple anatomical traits such as pit membrane, pit aperture or torus size. Highly cavitation resistant species exhibited both a high flexibility of the margo and a large overlap between the torus and the pit aperture, allowing the torus to tightly seal the pit aperture. These results support the hypothesis of seal capillary-seeding as the most likely mode of air-seeding, and suggest that the adhesion of the torus to the pit border may be the main determinant of cavitation resistance in conifers.

Occurrence of vestured pit is limited to some gnetophytes and angiosperms [95, 96]. Vesturing most commonly appears like small wartlike lobes within pit cavities but may also be present on pitting-free parts of vessel walls. Vestures are lignified and compressively strong. Thus, after Zweypfenning [97] vestures could function as mechanism that prevents or minimizes the deflection and the risk of rupture of the pit membrane, in case of pressure drop between adjacent vessel elements. The cavitation fatigue of the pit membrane would be minimized as well. The air seeding occurs trough membrane pores and there is no distortion of the membrane prior to air-seeding. However, vestured pits are not universal in dicotyledons nor of dry areas either cold areas and the benefit of vestures may only apply to a limited range of air seeding pressures [98].

Important feature of the xylem structure is its connectivity i.e. the fact that conduits are interconnected to form a network [53, 12]. Investigations on the spatial arrangement of conduits [99, 100] gave the support to define vascular system as a network integrating all main parts of the plant's body, i.e. roots, branches and leaves. According to the model presented by Loepfe et al. [101] the maximum hydraulic conductivity and vulnerability to embolism increase

with the connectivity of the xylem network. This can be explained by the fact that connectivity determines the fraction of all the potential paths or conduits actually available for both water transport and spread of embolisms. In the xylem, connectivity corresponds to the average number of different neighbor conduits to which a conduit is connected. According to the air seeding hypothesis, embolism propagates from an air-filled conduit to a functional one through the porous membrane that connects them. Thus the first condition for a conduit to be embolised is that it is connected to an air-filled conduit. The conduit will be more vulnerable to embolism the more connections it has, since more connected conduits will be more likely to be connected to an already air-filled conduit. At the tissue level high connectivity would facilitate the spread of emboli and therefore increase the vulnerability to drought induced embolism. An increase in conduit length, pit pore size or fraction of contact area occupied by pores resulted in an increment of maximal hydraulic conductivity in the presented model. The effect of conduit length on conductivity was not only through changing the number of pit membranes that water has to cross but also through a modification of the overall connectivity of the system. Earlier works also contributed to a prediction that if the gain of increased diameter of the conduit has to be fully realized in terms of conductivity it length should increase as well [102, 92]. However, there is a concept of 'saturating vessel length' above which there is no further increase in vessel conductivity and vessels longer than the saturating length contribute nothing to hydraulic conductivity being no mere that ways of embolism and disease spread [103, 92].

5. Short and long-term adjustments to water stress at different levels of woody plant organization

The continuity of water columns from soil throughout the plant linked to the evaporative flux at leaf cells is described as SPAC – soil-plant-atmosphere continuum. Maintenance of water column continuity is crucial to ensure water supply to leaves. Thus there is strong association between water transport capacity and the carbon gain by leaves which is due to the need of displaying large surface of hydrated cells in desiccating environment i.e. air. Any shortage in water supply in relation to requirements of the leaves results in water deficit and plant stress. Thus it is likely that leaf –level homeostasis in water status is maintained through ontogeny in conditions of varied and changing soil and atmosphere, possibly involving whole-plant changes in the resistance to liquid water flow [41]. In homeohydric plants i.e plants that can keep their internal water content relatively constant, regardless of the external environment, stomata exist to regulate plant water status by adjusting transpiration rate. Homehydric plants (i.e. ferns, gymnosperms, angiosperms) are further classified as either isohydric which have tight stomatal control and anisohydric with control less strict. In the initial stages of drought or for short-term drought conditions the response is always at the leaf level but differs between species between two theoretical extremes concerning perfectly isohydric plants that will close stomata reducing transpiration and simultaneously carbon gain to maintain the predrought leaf water status and perfect anisohydric plants that would keep stomata more open reducing leaf potential just enough to maintain leaf transpiration. An excellent exemplification of this

differential behavior are the results of Tandea and Sperry [64] work on cavitation resistance, vessel refilling, transport capacity and water status in ring-porous oak (*Quercus gambelii* Nutt.) and diffuse-porous maple (*Acer grandidentatum* Nutt.) that co-dominated summer-dry foothills in the western Rocky Mountains of the USA. It has been demonstrated that the large earlywood vessels of ring-porous trees can be extraordinarily vulnerable to cavitation making it necessary that these trees maintain a consistent and favorable water status. Native embolism measurements, dye perfusions and balance pressure exudation patterns indicated that the large earlywood vessels of 2–3-year-old oak stems cavitated extensively on a daily basis as predicted from laboratory vulnerability curves, resulting in a more than 80% reduction in hydraulic conductivity. Maple branches showed virtually no cavitation. Oak vessels refilled on a daily basis, despite negative xylem pressure in the transpiration stream, indicating active pressurization of embolized vessels. Conductivity and whole-tree water use in oak were between about one-half and two-thirds that in maple on a stem-area basis; but were similar or greater on a leaf-area basis. Oak maintained steady and modest negative xylem pressure potentials during the growing season despite little rainfall, indicating isohydric water status and reliance on deep soil water. Maple was markedly anisohydric and developed more negative pressure potentials during drought, suggesting use of shallower soilwater. Although ring porosity may have evolved as a mechanism for coping with winter freezing, this study suggests that it also has major consequences for xylem function during the growing season.

Common short-term respose to drouht is reduction in hydraulic conductivity of both xylary and extra-xylary pathways of water movement [104]. This reduction occurs not only as the consequence of xylem cavitation development but includes also interrupton of water flow at the soil-root interface, suberinization of root epidermal cells and down-regulation of aquaporin expression.

According to the model presented by Maseda and Fernández [41] the response to prolonged drought depends mainly on the type of leaf-level response and will include reduction of leaf area in anisohydric plant whereas isohydric ones should be able to keep it only little reduced. In the time scale close to an individual life span the adjustment to prevailing soil and atmosphere conditions are expected through developmental plasticity.

6. Conclusions

Facing a potentially lethal loss of hydraulic conductivity while draught periods vascular plants have developed structural and physiological mechanisms some of which can be categorized as embolism avoidance, embolism reversal and embolised conduits replacement through production of new xylem. Embolism avoidance is likely the first to act at the initial stages of draught; it requires a tight control of xylem pressure which plants can execute through stomatal control. Embolism reversal relays on the refilling with water of gas-filled conduits once cavitation event occurred. It can be driven by over atmospheric root/stem pressures originating in specific conditions at define period of the year or by local pressurization, while the neighboring conduits are under tension. There is evidence for daily cycles of cavitation

and refilling which is of great ecological importance in respect to photosynthetic capacity restoration. Production of new xylem conduits in aim to replace cavitated ones, requires carbon investment for growth processes, is common for maintaining hydraulic conductivity in plant that possesses the capacity for secondary growth e.g. trees and shrubs. Plants adopt one or more of these strategies, which are not alternative to one another. In woody plants there is evidence for all three strategies to occur, ensuring the conductivity restoration at different time and plant body organization scale. A number of ecophysiological features will determine whether a tree species can capture and maintain site dominance. Xylem anatomy and chemistry is among these strategic features and the compromises needed for mechanical support, hydraulic conduction, light interception and gas exchange are elements of life strategy. Experimental observations and theoretical modeling revealed that xylem embolism repair is a physiological process requiring fine coordination of sugar metabolism, solute and water transport and biochemical and morphological traits of conduits. In the light of these findings the image of xylem as an inert, vulnerable network of nonliving, pipe-like cells only passively transporting water by tension driving force seem inadequate. Xylem should rather be looked as a finely regulated water transport system tightly depending on plant life processes for optimal functioning and maintenance, especially under environmental stress conditions.

Acknowledgements

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