

MEELI ALBER

Impact of elevated atmospheric humidity
on the structure of the water transport
pathway in deciduous trees



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395

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Impact of elevated atmospheric humidity
on the structure of the water transport
pathway in deciduous trees



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Press

Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications which are referred to in the text by Roman numerals:

- I** Jasińska AK, **Alber M**, Tullus A, Rahi M, Sellin A. **2015**. Impact of elevated atmospheric humidity on anatomical and hydraulic traits of xylem in hybrid aspen. *Functional Plant Biology* **42**: 565–578.
- II** Sellin A, **Alber M**, Keinänen M, Kupper P, Lihavainen J, Löhmus K, Oksanen E, Söber A, Söber J, Tullus A. **2017**. Growth of northern deciduous trees under increasing atmospheric humidity: possible mechanisms behind the growth retardation. *Regional Environmental Change* **17**: 2135–2148.
- III** Sellin A, **Alber M**, Kupper P. **2017**. Increasing air humidity influences hydraulic efficiency but not functional vulnerability of xylem in hybrid aspen. *Journal of Plant Physiology* **219**: 28–36.
- IV** **Alber M**, Petit G, Sellin A. **2019**. Does elevated air humidity modify hydraulically relevant anatomical traits of wood in *Betula pendula*? *Trees – Structure and Function* **33**: 1361–1371
- V** Sellin A, Taneda H, **Alber M**. **2019**. Leaf structural and hydraulic adjustment with respect to air humidity and canopy position in silver birch (*Betula pendula*). *Journal of Plant Research* **132**: 369–381.
- VI** Sellin A, **Alber M**, Jasińska AK, Rosenvald K. **2022**. Adjustment of leaf anatomical and hydraulic traits across vertical canopy profiles of young broadleaved forest stands. *Trees – Structure and Function* **36**: 67–80.

Author’s contribution to the articles denotes: * a minor contribution, ** a moderate contribution, *** a major contribution.

	I	II	III	IV	V	VI
Original idea	*	*	*	**	**	*
Study design	*	*	*	**	**	*
Data collection	***	**	***	***	***	***
Data analysis	**	**	***	***	**	**
Manuscript preparation	*	**	*	***	**	*

LIST OF ABBREVIATIONS

A_{ap}	aperture area of bordered pit (μm^2)
AED	atmospheric evaporative demand
A_L	leaf area (m^2)
A_{pit}	pit membrane area (μm^2)
AQP	aquaporin
A_S	area of stomatal complex (μm^2)
A_{sw}	sapwood cross-sectional area (m^2)
A_v	vessel lumen area (μm^2)
A_X	cross-sectional area of xylem (m^2)
D_h	hydraulically weighted mean diameter of vessels (μm)
D_v	vessel diameter (μm)
FAHM	Free Air Humidity Manipulation experiment
g_c	canopy conductance to water vapour ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_{Smax}	maximum stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
HV	Huber value ($\text{m}^2 \text{m}^{-2}$)
HVSH	hydraulic vulnerability segmentation hypothesis
I_{vul}	xylem vulnerability index
K	hydraulic conductance ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
k	specific hydraulic conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)
K_B	branch hydraulic conductance ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_L	leaf hydraulic conductance ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_{lb}	hydraulic conductance of leaf blade ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_{max}	maximum hydraulic conductance ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
k_S	experimentally measured specific conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)
K_T	whole-plant hydraulic conductance ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
k_t	theoretical specific conductivity of xylem ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)
l	length of branch or stem segment (m)
l_{gc}	guard cell length (μm)
PD	density of bordered pits (mm^{-2})
PF	pit field fraction (%)
PLC	percentage loss of hydraulic conductivity (%)
RH	relative air humidity (%)
SD	stomatal density (mm^{-2})
SEM	scanning electron microscopy
SPI	stomatal pore area index
VA	relative area of vessels (%)
VD	vessel density (mm^{-2})
V_G	vessel grouping index
VLA_{min}	density of minor veins (mm mm^{-2})

VLA	total vein density (mm mm^{-2})
VPD	atmospheric vapour pressure deficit (kPa)
WUE	water-use efficiency
$\Delta\Psi$	water potential difference (MPa)
η	dynamic viscosity of water (Pa s)
ρ_w	density of water (kg m^{-3})
Ψ_L	leaf water potential (MPa)
Ψ_s	soil water potential (MPa)

1. INTRODUCTION

1.1. Pathway of water movement in plants and its anatomical structure

Plants can be treated as a hydraulic system transferring water from the soil to the atmosphere. The driving force of this transfer is the water potential gradient in the soil–plant–atmosphere continuum induced by transpiration, fuelled by solar radiation absorbed in vegetation. Transpiration is controlled by vapour pressure difference between the leaf interior and the free atmosphere and stomatal openness. Water moves from the soil through the roots and stem to the leaves along vascular pathways—xylem vessels and tracheids (Cruziat et al. 2002; Tyree and Zimmermann 2002). Xylem vessels and tracheids are tracheary elements that are highly specialized non-living cells at maturity. Both vessels and tracheids represent elongated hollow cells that have lignified walls with secondary thickenings (Kirkham 2005). Vessels consist of vessel members connected end to end via perforation plates and forming long conduits, while tracheids consist of single cells tapering at their ends and connecting laterally to each other (Zimmerman 1983).

Xylem elements form the largest part of plants' water transport system (Taiz and Zeiger 2010). A plant's hydraulic system allowing water movement in the liquid phase, plays a central role in the ability of the stomata to remain open and supports photosynthesis in mesophyll cells (Sack et al. 2015). Xylem anatomy differs among organs and largely impacts water movement in plants. The most relevant features at the cellular level are conduit diameter, length, cell wall characteristics, and the presence or absence of end walls. At the tissue level, the most essential traits are inter-conduit pitting and the number and distribution of the conduits (Kim et al. 2014). When the vessels' size increases, their number per area decreases as required to pack conduits into the available wood volume (Sperry et al. 2008; Savage et al. 2010).

Cavitation is the breakage of a continuous water column, which occurs when tension in the xylem conduit exceeds a certain threshold. Cavitation causes embolism, meaning that xylem conduits are filled with air and water vapour (Vilagrosa et al. 2012). Adjacent living parenchyma cells provide water and energy for the refilling process (Secchi and Zwieniecki 2012). Living cells neighbouring the embolized vessel create a driving force, causing water to flow into the vessel lumen, pressurizing the gas, which dissolves in xylem fluid and diffuses away from the vessel (Vesala et al. 2003). The parenchyma plays a determining role in springtime pressurization of the xylem vessels and sap flow, which is common in birches and maples, via creating osmotic gradients (Hölttä et al. 2018).

1.2. Ecophysiological consequences of plant hydraulic conductance

There are several characteristics of plant hydraulic systems that determine how easily water can move in plants. Hydraulic conductance (K), expressed as water flux divided by the driving force (i.e. water potential gradient from soil to leaf), characterizes water conduction efficiency within plants, whereas it can be measured/calculated for separate sections of the transport pathway (Tyree and Ewers 1991; Cruiziat et al. 2002):

$$K = \frac{F}{\Delta\Psi} \quad (1)$$

where F is the volume flow rate (mmol s^{-1}), and $\Delta\Psi$ is the water potential drop across a particular segment (MPa).

In experimental systems, the driving force to push/pull water through plant segments can be generated by applying pressure, centrifugal force, gravity feed or a vacuum (Alder et al. 1997; Cruiziat et al. 2002; Li et al. 2008). Hydraulic conductance of the whole plant (K_T) estimates total water movement capacity through the plant. Hydraulic resistance (R) is expressed as reciprocal of hydraulic conductance ($1/K$); whole-plant hydraulic resistance can be partitioned into components corresponding to different plant organs. The specific hydraulic conductivity (k) characterizes the water-transport efficiency of the conducting tissues considering size effects; thus, it is most commonly expressed per unit sapwood area (Cruiziat et al. 2002). In stems, it primarily depends on porosity of the xylem (Tyree and Ewers 1991).

A widely evidenced phenomenon is a trade-off between hydraulic efficiency and the functional safety of the xylem (Sperry 2003; Hacke et al. 2006; Gleason et al. 2016). On the one hand, plants benefit from high hydraulic conductivity provided with wide and long vessels, but on the other hand, they should avoid being at risk of massive embolism due to large vessels (Hacke and Sperry 2001; Sperry et al. 2008). Plants that often experience higher levels of water stress are more resistant to cavitation than plants whose water status always remains favourable (Hacke 2015a).

Hierarchical design of the water transport system and hydraulic segmentation between proximal and distal organs has been hypothesized to be an important protective mechanism for plants to minimize the detrimental effects of drought-induced hydraulic failure (Liu et al. 2015). Differential cavitation resistance of plant segments helps plants to survive during severe droughts by the eventual shedding of expendable organs (Tsuda and Tyree 1997). According to the hydraulic vulnerability segmentation hypothesis (HVSH; Tyree and Ewers 1991), plants are hydraulically designed to sacrifice highly vulnerable plant distal segments to keep the remaining basal parts hydraulically active. Distal portions of trees should be more susceptible to hydraulic dysfunction than boles due to high hydraulic resistance at organ connections, resulting in steep pressure gradients. In fact, roots

and especially leaves are commonly more vulnerable to embolism compared to branches and trunks, while branches are more resistant to embolism than trunks (Johnson et al. 2016; Savi et al. 2016; Scoffoni et al. 2017b). Leaves will embolize before stems to protect the functionally more valuable conducting tissues of stems against more negative water potential (Wolfe et al. 2016). Klepsch et al. (2018) published data challenging the HVSH; xylem in leaves and branches had similar resistance to embolism, and leaves of *Betula pendula* had higher resistance to embolism than its branches. The last finding could be attributed to thicker pit membranes in the xylem of leaves. This discrepancy can be explained by the fact that HVSH is more characteristic for species from arid regions than humid regions (Zhu et al. 2016).

High plant hydraulic conductance is a precondition for high carbon gain and tree productivity (Tyree 2003). The higher water transport capacity of stems and branches enables higher stomatal conductance and consequent photosynthetic rates, and this in turn supports potentially higher growth rates (Brodribb et al. 2002; Meinzer et al. 2010; Islam et al. 2018). Maximum transpiration rates are related to the maximum values of K_T (Tsuda and Tyree 2000). Rodríguez-Gamir et al. (2016) found that whole-plant transpiration and hydraulic conductance, which depend on root and shoot hydraulic conductance, are positively correlated. Presumably, plant water transport capacity (leaf-specific hydraulic conductance) is coordinated with leaf-level gas exchange capacity (Rodríguez-Gamir et al. 2016).

As a tree grows taller, its hydraulic resistance also increases due to a longer water transport pathway accompanied by a greater water potential drop and a decline in the water status of the top leaves. Water shortage in leaves forces stomata to close, and it starts to limit photosynthesis and growth even at sufficient soil moisture (Ryan and Yoder 1997; Koch et al. 2004). Liu et al. (2019a) found that taller woody species have higher xylem conductivity to compensate for the high evaporative demand and the longer transport pathway. To minimize resistance to water transport from roots to leaves, trees have evolved a network of xylem conduits with tapering structure, i.e. conduits narrow apically throughout their roots, stems and branches (Anfodillo et al. 2006). To maintain similar conductivity, an increase in the number of xylem vessels per unit cross-sectional area is necessary if conduits become narrower (Kim et al. 2014). Within leaves, the same trend continues in the distal direction; xylem conduit diameters decrease from the petiole to the midrib and further to minor veins (Coomes et al. 2008). The distal tapering of xylem vessels is a universal trait that reduces the effect of tree height on the total path-length resistance (Anfodillo et al. 2013). In older and taller trees, the area of sapwood increases, causing higher maintenance respiration costs, and less energy remains for height growth (Ryan and Yoder 1997; West 2020). Hence, their hydraulic resistance (Ryan and Yoder 1997) determines trees' maximum height.

Hydraulic conductance is associated with plant water-use efficiency (WUE). Water-use efficiency that expresses a balance between carbon gain and water loss can be estimated at different levels—on individual leaf, plant, stand or ecosystem scales (Guerrieri et al. 2019). WUE is driven by the anatomy of the water

transport pathway and factors that regulate hydraulic properties (Bramley et al. 2013). Both the stem and leaf hydraulic conductance of mulberry trees (*Morus* spp.) grown in water stress conditions are inversely correlated with WUE (Reddy et al. 2017). The shade foliage of *Betula pendula* is characterized by higher intrinsic WUE than sun foliage, which is associated with more conservative stomatal behaviour and lower K_T and leaf hydraulic conductance (Sellin et al. 2010). Kocacinar et al. (2008) showed that more water-use efficient C₄ species are characterised by lower leaf-specific hydraulic conductivity.

The importance of plant hydraulics among biological and environmental sciences is continuously increasing. Hydraulic traits mediate the ways in which plants interact with their abiotic and biotic environment; plant hydraulic properties are important in describing the function of ecological communities and ecosystems, and plant hydraulics is increasingly recognized as a central hub within a network by which plant biology is connected to paleobiology, agronomy, climatology, forestry, community and ecosystem ecology, and earth-system science (Sack et al. 2016). The hydraulic approach is increasingly applied to study the effects of climate change on forest ecosystems (McDowell and Allen 2015). Trees' hydraulic properties can be scaled up to the canopy or stand level. Canopy conductance (g_C) declines with increasing atmospheric vapour pressure deficit, in accordance with the inverse function (McDowell and Allen 2015):

$$g_C = \frac{A_{sw} \cdot k_S \cdot (\Psi_S - \Psi_L)}{h \cdot \eta \cdot A_L \cdot VPD} \quad (2)$$

in which A_{sw} is the conducting area of xylem (cm²), A_L is leaf area (m²), k_S is specific conductivity (m s⁻¹), h is plant height (m; a surrogate for total hydraulic path length), η is dynamic viscosity of water (Pa s), $\Psi_S - \Psi_L$ is the soil-to-leaf water potential difference, and VPD is vapour pressure deficit (kPa). If a constant g_C is assumed, then the hydraulic parameters that must shift to accommodate the higher evaporative demand include reductions in tree height, leaf area, or $A_L:A_{sw}$, and increases in hydraulic conductance and soil-to-leaf water potential gradient. Therefore, the hydraulic corollary to Darcy's law is used to predict characteristics of plants that will survive and die during drought under warmer future climates. Finally, the contribution of trees' water transport system to the global water cycle should not be underestimated. Approximately 62,000 km³ of water per year flows through the hydraulic pathways inside plants, which comprises 80–90% of the total terrestrial evapotranspiration (Jasechko et al. 2013).

1.3. Anatomical structure—a primary factor determining xylem water transport efficiency

The hydraulic conductivity of a capillary is described by the Hagen–Poiseuille law (Tyree and Zimmermann 2002):

$$K_{\text{capillary}} = \frac{r^4 \cdot \pi}{8\eta} \quad (3)$$

where r is the capillary radius (m) and η is the dynamic viscosity of water (Pa s). According to the Hagen–Poiseuille equation, the water transport efficiency of a xylem conduit is proportional to the fourth power of its diameter (Tyree and Ewers 1991; Pickard and Melcher 2005). Consequently, small shifts in the conduit radius are translated to substantial changes in its hydraulic conductivity. Altogether, both trees' water conduction capacity and cavitation resistance are primarily determined by xylem anatomy (Sperry et al. 2006). A higher growth rate accompanies greater vessel size and increased hydraulic conductivity because more efficient water transport enables higher stomatal conductance and photosynthetic rates and thereby supports an increased growth rate (Poorter et al. 2010; Fan et al. 2012).

Hydraulic conductance and vessel density are negatively correlated because of the inverse relationship between vessel area and vessel density (Sellin et al. 2008; Fan et al. 2012; Hietz et al. 2017). The greater the vessel area on the xylem cross-section, the higher its hydraulic conductivity (Jacobsen et al. 2007; Fan et al. 2012). However, increased vessel density cannot compensate for the effect of smaller vessel diameters on hydraulic conductivity (Zheng et al. 2019). The total area occupied by vessels may be larger if the plant has many small vessels, but hydraulic conductance is higher in plants with few large vessels, even though their total vessel area is smaller (Zanne et al. 2010; Hietz et al. 2017). In addition to the vessel diameter, its length is also a highly relevant trait; hydraulic conductance decreases with decreasing conduit length (Tyree and Ewers 1991). Shorter vessels have more end walls than longer ones, resulting in higher end wall resistivity (Ooeda et al. 2018).

The passage from conduit to conduit occurs through bordered pits, which are responsible for most of the resistance along the hydraulic pathway (Sperry et al. 2006; Choat et al. 2008). The pit membranes of angiosperm species have very high porosity. It has been suggested that pit membranes enable water transport under negative pressure by producing stable, surfactant-coated nanobubbles, while preventing the entry of large bubbles that would cause embolism (Kaack et al. 2019). Hydraulic conductance decreases with decreasing pit membrane porosity (Tyree and Ewers 1991), but at the same time, thick pit membranes tend to show higher embolism resistance than thin membranes (Li et al. 2016; Trueba et al. 2019). Pfautsch et al. (2018) found that larger vessels have thicker pit membranes. The pit membrane thickness may affect the size, length and shape of the pit membrane pores. The pit membrane pore size directly determines the air-seeding pressure between functional and non-functional vessels (Li et al. 2016).

In tropical *Ficus* species, experiencing frequent drought conditions in their habitats, greater intervessel pits have been reported (Li et al. 2019). The hydraulic conductivity of their sapwood is inversely correlated with pit aperture area and diameter and with the diameter of the pit membrane. This negative correlation can be explained by the trade-off between pit size and density. More drought-tolerant species have fewer pits and thus overall less water flow, while less drought-tolerant species have smaller pit membrane and/or aperture areas and higher pit densities to facilitate water transport in the xylem (Li et al. 2019).

Species with higher conduit-to-conduit connectivity exhibit higher xylem hydraulic conductivity but also increased vulnerability to embolism (Martínez-Vilalta et al. 2012). Jupa et al. (2021) demonstrated that angiosperm tree species, despite remarkable adjustments in vessel dimensions and densities upon water availability, exhibit surprisingly invariant intervessel lateral contact architecture. Vessel connectivity impacts hydraulic conductance by its relationship with embolism, as higher connectivity increases the likelihood of embolized vessels being bypassed. Highly connected vessels are usually the longest and widest within a particular plant tissue and have large mean intervessel pit areas and more likely possess large pores in their pit membranes, allowing easier bubble propagation (Mrad et al. 2018). Hochberg et al. (2017) showed that basal leaves are more vulnerable to embolism than apical leaves, probably due to their longer xylem vessels and higher connectivity.

Cavitation and formation of emboli in xylem conduits reduce the hydraulic conductance of roots, stems and leaves (Tyree and Sperry 1989; Milburn 1993), which limit stomatal openness and the transpiration rate (Nardini and Salleo 2000; Hacke and Sperry 2001). A high level of embolism reduces the capacity of trees to photosynthesize (Zwieniecki and Secchi 2015). Plants more resistant to cavitation have smaller vessel diameters, increased vessel wall thicknesses and exhibit higher values of conduit wall reinforcement $(t/b)^2$, where t is intervessel wall thickness and b is conduit wall span (Awad et al. 2010). The distribution of air bubbles presumes an air-filled conduit that has connections with other xylem elements and the pits containing sufficiently large pores. In the case of longer conduits, there is a higher probability that its neighbouring conduits are filled with air or that it has pits with larger pores (Loepfe et al. 2007). Cell age is also a relevant factor; cavitation induced by water stress develops earlier in 1–2-year-old xylem than in the current-year xylem (Fukuda et al. 2015).

1.4. Structural effects on the liquid and gaseous phase conductance of leaves

Water movement in leaves depends on the structure of the vein network, vascular bundles and xylem cells in vascular bundles (Sack and Holbrook 2006). Minor veins make up the majority (> 80%) of the total vein length (Sack et al. 2012; Mediavilla et al. 2020). Leaf hydraulic conductance (K_L) is strongly correlated

with minor vein length and total vein length expressed per lamina area unit, i.e. vein density (Sack et al. 2015). In leaves of *Acer saccharum* and *Quercus rubra*, minor veins constitute 32 and 49%, major veins 18 and 21%, petiole 14 and 4%, and outside-xylem pathway 36 and 26% of the total leaf hydraulic resistance, respectively (Sack et al. 2004). Minor veins also have a strong association with leaf water deficit tolerance; Hochberg et al. (2017) showed that minor veins cavitate after midrib cavitation. The density of minor veins is positively correlated with lamina tissue density and leaf dry matter content and negatively correlated with lamina thickness (Kawai and Okada 2018). Thin leaves provide shorter distances for the transport of water to evaporation sites, and this compensates for small vein density, as shown for Mediterranean oak seedlings (Mediavilla et al. 2021).

Water exits small veins as liquid and continues moving along the water potential gradient in the extravascular pathway outside the xylem to the epidermis, where it exits the leaf through stomata as a vapour (Rockwell et al. 2014). Inside the leaf, water mainly evaporates from the mesophyll cell surface but to a lesser extent from the epidermis and bundle sheath (Rockwell et al. 2014; Buckley et al. 2015, 2017). Higher vein length per unit area enhances hydraulic conductance of outside-xylem pathways (Buckley et al. 2015). Lignin deposition on bundle sheath cells of minor veins reduces conductance from the xylem to the mesophyll (Ohtsuka et al. 2018). Outside-xylem conductivity decreases with spongy mesophyll protoplast size and increases with the airspace fraction, mesophyll cell wall thickness and mesophyll cell surface area (Buckley et al. 2015; Xiong et al. 2017). In this pathway, water moves symplastically from cell to cell, depending on plasmodesmata connectivity. Plasmodesmata represent nanopores that serve as channels for molecular cell-to-cell transport (Christensen et al. 2021). In the extravascular pathway, water must pass through cell membranes; aquaporins (AQPs) play a significant role in this process by controlling the permeability of membranes (Sack et al. 2015). AQPs are integral membrane proteins from a larger family of major intrinsic proteins that form nanopores (also called water channels) in the membrane of biological cells, mainly facilitating the transport of water between cells.

Stomatal characteristics, especially stomatal size, impact water flux throughout the plant (Sack et al. 2003). Stomatal size determines pore area, and this largely explains the variation in transpiration; bigger stomata provide bigger pore areas (Giday et al. 2013). Smaller stomata may have shorter response times due to their greater cell membrane surface area to volume ratio and bigger stomata, longer response times to changes in the surrounding environment (Drake et al. 2013). Therefore, species with higher stomatal density and smaller guard cells demonstrate higher stomatal sensitivity (Drake et al. 2013; Lawson and Blatt 2014). Plants with slower stomatal dynamics may suffer from water deficits induced in drought conditions (Hetherington and Woodward 2003). Brodribb and Jordan (2011) showed that the development of stomata and leaf veins are coordinated, and due to this, gas exchange and hydraulic processes are also strongly

related to each other. Leaf liquid and gaseous phase conductance should be coordinated to keep stomata open and avoid tissue dehydration. The stomatal pore area index (SPI), a dimensionless index of stomatal pore area per lamina area, is related to leaf lamina thickness and correlates with leaf hydraulic conductance (Sack et al. 2003, 2005). Brocious and Hacke (2016) pointed out that traits of the petiole xylem in poplar leaves have a stronger impact on stomatal conductance compared to the xylem of the leaf lamina. Sellin et al. (2014) reported that maximum stomatal conductance to water vapour and mean net photosynthesis of trees are positively related to hydraulic conductance of the soil–leaf continuum.

1.5. Impact of environmental conditions on the structure of the water transport pathway

Light conditions have a multifaceted effect on the structure of the water transport pathway. Well-illuminated leaves and petioles have more xylem, bigger diameters of xylem elements and higher vein densities in leaf laminae and thus exhibit higher conductivities (Schultz and Matthews 1993; Sack and Frole 2006; Dayer et al. 2017). Higher irradiance after canopy release induces an increase in the vessel diameter of the stem xylem, which helps to cope with increased evaporative demand as a consequence of changed environmental conditions (Noyer et al. 2017). Light also affects stomatal morphology, although the trends may be inconsistent for different species. Sun leaves generally have higher stomatal densities than shade leaves (Brodrribb and Jordan 2011; Martins et al. 2014; Kardiman and Ræbild 2018). Kardiman and Ræbild (2018) reported that some rainforest species have larger and some smaller stomata when exposed to full sunlight, while other studies (Brodrribb and Jordan 2011; Martins et al. 2014) reported small or no changes in stomatal size. In mesic forests, the water supply for trees is not usually limited, but light is, and bigger vessels (i.e. efficient water supply) favour carbon uptake and enable better light competition (Pfautsch et al. 2016).

Plants growing in water deficit conditions commonly have narrow vessels spaced at higher densities (De Micco et al. 2008; Fichot et al. 2009; Olson and Rosell 2013). To minimize the decrease in hydraulic capacity due to smaller vessel size, plants increase the vessel number, i.e. vessel density. Vessel density is a more plastic trait than vessel diameter, and this helps to maintain a constant conducting area (Fichot et al. 2009). A decrease in water availability causes an increased pit membrane thickness (Schuldt et al. 2016), providing higher embolism resistance compared to thin membranes (Li et al. 2016). In areas where drought is frequent, plants have a more cavitation-resistant hydraulic system, which is less efficient in water transport and thus limits growth; thus, such a design is not beneficial for plants from regions with sufficient water availability (Bourne et al. 2017). Cavitation and consequent embolism of xylem elements can be induced by tissue dehydration as a result of water deficit or by freezing. The radius of vessels has a greater impact on freezing-induced embolism than on

drought-induced embolism, where a very important factor is the structure of intervessel pits (Hacke and Sperry 2001). When xylem sap freezes, dissolved gases come out of the solution and form air bubbles. In large xylem conduits, bubbles can merge, and the conduit will become fully embolized. Drought-induced cavitation occurs when air is sucked through pit pores into a functioning water-filled conduit. This phenomenon occurs when the pressure differences between xylem water and the surrounding air exceed the capillary forces at the air–water interface (Hacke and Sperry 2001).

Previous studies have shown that plants grown in environments with high air humidity usually have bigger stomata (Hetherington and Woodward 2003; Nejad and Meeteren 2005; Fanourakis et al. 2020). Leaves grown in high humidity have bigger epidermal cells and longer guard cells, forming bigger stomata (Nejad and Meeteren 2005; Brodribb et al. 2013). Less is known about how xylem traits respond to high precipitation, higher air humidity or flooding. Different studies have reported contradictory results. The diameter of xylem conduits in different conifer species responds to flooding variously; the diameter increased in *Thuja orientalis* and *Cryptomeria japonica*, remained unchanged in *Pinus halepensis* and decreased in *Pinus densiflora* (Kozłowski 1997). In a growth chamber experiment, where *Pinus ponderosa* and *Pseudotsuga menziesii* were grown in high and low relative humidity and then moved to low or high humidity environments, respectively, the changed humidity conditions had no impact on tracheid lumen area (Szejner et al. 2020). Flooding causes smaller and more numerous vessels in *Quercus robur* (Copini et al. 2016) and *Fraxinus nigra* (Tardif et al. 2021).

An increase in nutrient availability (especially nitrogen) stimulates the growth rate, resulting in wider and more grouped vessels that enable higher hydraulic conductivities (Hacke et al. 2010; Spann et al. 2016). Pygmy plants grown under harsh nutrient limitations have reduced conduit diameter and structurally weaker vessel and libriform fibre walls (Cary et al. 2020). Weaker cell walls collapse more easily under high tension in the case of water stress, increasing resistance to water movement in the xylem (Cochard et al. 2004).

In addition to the cell dimensions, environmental conditions can modify proportions of separate tissues in plant organs. Leaf hydraulic conductance is positively correlated with lamina thickness (Xiong et al. 2015), especially with the thickness of the upper epidermis, palisade mesophyll and palisade/spongy mesophyll ratio (Sack and Frole 2006; Chen et al. 2009). Leaves acclimated to a higher irradiance tend to be thicker and exhibit a higher conductance (Sack et al. 2015). Previous studies have shown that plants grown under water deficit have a higher density of pith rays and a larger number of cells in the ray parenchyma of stems (Esteban et al. 2012; Fonti et al. 2013). This acclimation enables plants to store greater amounts of non-structural carbohydrates, which helps them to survive stress. Olano et al. (2013) found that more precipitation in May and August promotes the development of parenchyma in Mediterranean trees. However, more parenchyma cells bring about higher maintenance respiration costs, which takes place in all living tissues, including the parenchyma (Ryan 1990; Kozłowski and Pallardy 1997).

1.6. Aims of this dissertation

Weather models have predicted that the amount of precipitation will increase in northern Europe during this century (Kont et al. 2003; Dai 2006; IPCC 2013, 2021). In Estonia, monthly precipitation during 1966–2015 has increased in January, February and June, whereas summer precipitation increased 12.3 mm per decade (Jaagus et al. 2018). Climate simulations predicting for the period 2071–2100 estimated a rise in annual precipitation of 4 to 34% in Northern Europe compared to the period 1971–2000 (Jacob et al. 2014). Jacob et al. (2014) also highlighted the increase in heavy precipitation events. For Estonia, different models predict a change in the mean monthly precipitation of 9–22% in winter, 10–24% in spring, 11–19% in summer, 8–12% in autumn and an annually average of 10–19% (Luhamaa et al. 2014). The rise in precipitation frequency is accompanied by an increase in relative air humidity (RH) on regional and local scales (Fanourakis et al. 2020). RH in the warm season increased up to 10% per decade in northern Europe, Asia and some regions of Canada over the period 1979–2014 (Vicente-Serrano et al. 2018). Increasing atmospheric humidity reduces water fluxes through vegetation, influencing plants' structure and function. Kopper et al. (2011) demonstrated that elevated air humidity decreases the vapour pressure gradient between leaf interior and surrounding air, causing decreased sap flow.

To study the impact of increasing air humidity on trees' structure and functioning, the Free Air Humidity Manipulation (FAHM) facility has been established in eastern Estonia. Data for the doctoral thesis were collected at the FAHM site from two commercially important deciduous tree species—hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) and silver birch (*Betula pendula* Roth). Along with anatomical analysis, hydraulic and gas exchange measurements were carried out on the same trees. It enabled the analysis of how anatomical changes in tree water transport system influence plant water relations, gas exchange and growth rate.

The aim of this doctoral thesis was to test the following hypotheses:

- 1) Elevated relative air humidity induces changes in xylem anatomy, which leads to lower hydraulic efficiency of stems and leaves (**I, III–VI**).
- 2) Increasing atmospheric humidity will induce alterations in the structure of both xylem cells and stomata, which potentially increase the risk of cavitation and might become critical in case of weather extremes (severe drought, heat wave) (**III, V, VI**).
- 3) Further increases in atmospheric humidity in the moderately humid climate of Estonia changes proportions of different xylem tissue types; we presumed that increased humidity would increase the share of parenchyma (**II**).

2. MATERIALS AND METHODS

2.1. Description of the study site and sample trees

Fieldwork was conducted at the Free Air Humidity Manipulation (FAHM) facility situated in Rõka village (58°14'N, 27°29'E), eastern Estonia. An experimental forest plantation of the FAHM site was established to study the effects of increasing atmospheric humidity on forest ecosystems. The FAHM system enables air relative humidity (RH) to be elevated up to 18% compared to the ambient level, while the mean increase in RH across the growing season is ~7%. Humidification was applied during the day, six days a week throughout the growing season. The experimental plots were planted with two deciduous tree species: silver birch (*Betula pendula* Roth) and hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.). A detailed description of the FAHM site and its technical setup, climate and soil characteristics have been presented in Kupper et al. (2011).

In Papers **I** and **VI**, hydraulic measurements and wood sampling were performed on 6-year-old saplings of hybrid aspens. The measurements were conducted on nine trees from the plots with artificially elevated RH (**H** treatment) and nine trees from the control plots (**C** treatment) in July–August 2011. The average height of trees was 4.80 ± 0.19 m in the **C** plots and 4.52 ± 0.17 m in the **H** plots. The sample branches were cut from three heights in the canopy. After hydraulic measurements, four to six healthy leaves from each branch were sampled randomly. From leaves, traits of the vascular bundles, mesophyll, venation and stomata were measured. Additionally, two petioles per branch were sampled randomly.

In Papers **II** and **III**, hydraulic and anatomic measurements were performed on 1-year-old hybrid aspen coppice (root and stump sprouts) on 46 trees in **C** plots and 47 trees in **H** plots in July 2014. The mean height of trees was 2.31 ± 0.04 and 1.99 ± 0.05 m in **C** and **H** plots, respectively. Stem samples were taken at a mean height of 60 cm above the ground.

In Papers **IV** and **V**, hydraulic measurements and wood sampling were performed on 4-year-old saplings of silver birch in three **H** and three **C** plots from July to August 2009 on two trees from each experimental plot. The mean height of trees was 3.76 ± 0.10 m in **C** plots and 3.25 ± 0.12 m in **H** plots. Three branches from each tree were cut from three heights. After hydraulic measurements, six healthy leaves from each branch were sampled randomly: two leaves for stomatal impressions, two for vascular bundle and mesophyll traits and two for vein density measurements. Additionally, two petioles per branch were chosen randomly.

2.2. Hydraulic measurements using the high pressure method

The hydraulic conductance of branch segments, branch components (leafless branch, petioles, leaf blades) and stem segments were measured using a high pressure flow meter (HPFM; Dynamax, Houston, TX) applied in a quasi-steady-state mode (**I**, **IV–VI**) or in transient mode, raising the pressure from 0 to 0.05 MPa (**III**). Data on hydraulic traits were corrected for the dynamic viscosity of water and expressed per unit leaf area. The total area of the leaf blades was measured with a LI-3100C optical area meter (Li-Cor Biosciences, Lincoln, NE).

The specific conductivity (k_s ; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) of the branch and stem xylem was calculated as follows:

$$k_s = \frac{K_{\text{seg}} \cdot l}{A_x} \quad (4)$$

where K_{seg} is the hydraulic conductance of the branch or stem segment, l is the length of the segment, and A_x is the cross-sectional area of the xylem.

2.3. Determination of xylem cavitation susceptibility

In paper **III**, stem segments >20 cm in length were cut from below the crown base of aspen coppice shoots, packed in plastic bags, transported to the field lab, recut underwater to a length of 14 cm (all within 3–4 min), and measured immediately for initial hydraulic conductance (K_{in}). Subsequently, the specimens were placed into a cavitation chamber attached to a Model 600-EXP pressure chamber (PMS Instrument Company, Albany, OR). Cavitation of the stem segments was induced using an air-injection technique applying a pressure (P_c) of 1.0, 1.5 or 2.0 MPa for one hour, and the hydraulic conductance of the embolized stem segments (K_{cav}) was measured at low pressure. The specimens were then flushed with filtered, deionized and freshly degassed water at a pressure of 0.3 MPa for 10 min to remove air bubbles from embolized vessels, measured hydraulically again, flushed for an additional 10 min and measured once more. The greater value of the last two measurements was taken as the maximum hydraulic conductance (K_{max}). Respective values of specific hydraulic conductivity of the xylem (k_{in} , k_{cav} and k_{max}) were calculated according to equation (4). The percentage loss of hydraulic conductivity because of native embolism (PLC_{nat}) and artificially induced cavitation ($\text{PLC}_{1.0}$, $\text{PLC}_{1.5}$ or $\text{PLC}_{2.0}$) was calculated as:

$$\text{PLC} = \frac{100 \cdot (k_{\text{max}} - k)}{k_{\text{max}}} \quad (5)$$

2.4. Preparing microscope slides and performing light and scanning electron microscopy

The oven-dried stem and branchwood samples were softened in ethanol and glycerine solution (I–III) or boiled in water. The soft samples were processed in an ethanol gradient and treated in BioClear (BioOptica, Milan, Italy) and a liquid paraffin for tissue embedding (IV). Cross-sections (I, III, IV) or tangential sections (II) were cut with a SM2000R sliding microtome (Leica Microsystems, Nussloch, Germany) or rotary microtome (Leica RM2145, Leica Microsystems). The slices were stained with safranin (I), a mixture of Alcian blue and safranin (II, III) or a solution of safranin and astra blue (IV). Stained sections were rinsed with water, ethanol and xylol. Samples were mounted in Canada balsam (I–III) or Eukitt (BioOptica, Milan, Italy) (IV).

For studying pit traits of stem xylem cells, scanning electron microscopy (SEM) was applied (I). Oven-dried stemwood specimens were split in a radial direction and fixed on a stub with carbon-based adhesive discs. The slices were coated with gold in a modified sputter-coating device (VUP-4; Moscow, Russia). All samples were examined with a Zeiss EVO LS15 scanning electron microscope (Carl Zeiss Microscopy, Jena, Germany).

To prepare leaf samples (V, VI), the pieces of laminae and petioles were fixed in a solution of formaldehyde, acetic acid, ethanol and then dehydrated in an ethanol gradient. For embedding samples passed through a series of isopropanol, Roti-Histol and Roti-Plast solutions. Cross-sections were cut with a SM2000R microtome and stained with Fast Green and safranin. Samples were rinsed with water, ethanol and xylol and mounted in Canada balsam. For vein density measurements, leaves were held in a solution of NaOH and stained with toluidine blue (V, VI). Stomatal imprints were made using a clear nail polish and adhesive tape (V). In paper VI, the SEM technique was applied to measure stomatal traits on leaf samples fixed in glutaraldehyde, dehydrated in an ethanol gradient, critical point-dried in CO₂ and coated with a thin layer of gold in a sputter coating system (VUP-4). The samples were photographed with an LEO 1430VP scanning electron microscope (Leo Electron Microscopy, Cambridge, UK).

Light microscope images of wood and leaf samples were obtained with a Nikon Eclipse 50 microscope (Nikon Corp., Tokyo, Japan) and photographed with a digital camera (DS-Fi1, Nikon Corp.). The images were analysed with ImageJ (National Institutes of Health, Bethesda, MD) or WinCELL software (Regent Instruments, Sainte-Foy, Canada). Based on the anatomical measurements, the following quantitative traits were calculated.

- Vessel grouping index (V_G):

$$V_G = \frac{N_t}{N_s + N_g} \quad (6)$$

where N_t is the total number of vessels, N_s is the number of solitary vessels and N_g is the number of vessel groups (Carlquist 2001). The mean vessel diameter (D_v) was calculated as a geometric mean of the minor and major perpendicular lumen diameters. The relative area of vessels (VA) was expressed as a percentage of the xylem cross-sectional area occupied by the total area of vessel lumina.

- The vulnerability index (I_{vul}), expressed as mean D_v divided by vessel density (VD), was used as a rough estimate of embolism susceptibility (Arbellay et al. 2012). Greater values of I_{vul} indicate higher xylem functional vulnerability to water stress.
- Based on Sperry's concept (Sperry et al. 1994), we calculated a hydraulically weighted mean diameter (D_h) for each sample:

$$D_h = \frac{\sum_{i=1}^n (\sqrt{a_i \cdot b_i})^5}{\sum_{i=1}^n (\sqrt{a_i \cdot b_i})^4} \quad (7)$$

where a_i and b_i are the minor and major perpendicular lumen diameters of the i th vessel.

- Theoretical specific conductivity of the xylem (k_t ; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$), an index of xylem conducting efficiency expressed per sapwood transverse area, was calculated according to Lewis and Boose (1995):

$$k_t = \frac{\pi \rho_w}{64 \eta A_x} \sum_{i=1}^n \frac{a_i^3 \cdot b_i^3}{a_i^2 + b_i^2} \quad (8)$$

where ρ_w is the density of water (kg m^{-3}), A_x is the sampled cross-sectional area of xylem (m^2) and η is the dynamic viscosity of water (MPa s).

In paper **II**, the parenchyma volume index ($\mu\text{m}^3 \text{mm}^{-2}$) was calculated as an area of parenchyma rays per cross-section multiplied by mean ray height in tangential view.

2.5. Data analyses

Statistical data analyses were carried out using Statistica, Ver. 7.1 (StatSoft Inc., Tulsa, OK). Hydraulic and anatomical characteristics were examined using linear mixed models regarding the effects of ‘Treatment’, ‘Experimental plot’ (nested in the first) and ‘Branch/sample position’ and physiologically relevant covariates (tree height, stem diameter, sample height, etc.). ‘Treatment’ and ‘Sample position’ were treated as fixed factors and ‘Experimental plot’ as a random factor. Statistically insignificant covariates were removed step-by-step from the analysis models, and the final model was selected according to R^2 and error terms. Type III or IV sums of squares were used in the calculations, and post hoc mean comparisons were conducted using Tukey’s HSD test. Bivariate relationships between the studied characteristics and independent variables were assessed using Pearson correlation coefficient (r) or least squares regression. Allometric relationships between trees’ biometric traits (**III**) were analysed by standardized major axis (SMA) regression using SMATR, Vers. 2.0 freeware (<http://bio.mq.edu.au/research/groups/comparative/SMATR/>).

3. RESULTS AND DISCUSSION

3.1. Changes in the anatomical structure of xylem and stem/branch hydraulic properties

It is well known that various environmental factors can affect xylem anatomy (Hacke 2015b). The FAHM experiment demonstrated that the manipulation of air humidity causes changes in xylem properties. The relative vessel area (VA) and vessel density (VD) of hybrid aspen stems (**I**) decreased in response to elevated air humidity (Figure 1 and Table 1). These anatomical changes suggest that in humidification treatment, trees have functionally less efficient conductive area. Trees grown in elevated air humidity conditions experience reduced transpirational water flux because of the lower atmospheric evaporative demand (AED; Kupper et al. 2011; Tullus et al. 2012). Thus, growing in more humid air, trees do not experience strong environmental pressure for the development of an efficient water transport system (Carlquist 2001; Tyree and Zimmermann, 2002). The effects of wet soil conditions and waterlogging on xylem structure that have been previously studied are analogical. White spruces grown in unfavourable and stressful wet soil conditions have reduced tracheid lumen area (Lange et al. 2020). Bhusal et al. (2020) found that apple cultivars grown in water-logged conditions exhibited decreased vessel density and vessel diameter, which resulted in reduced xylem hydraulic conductivity.

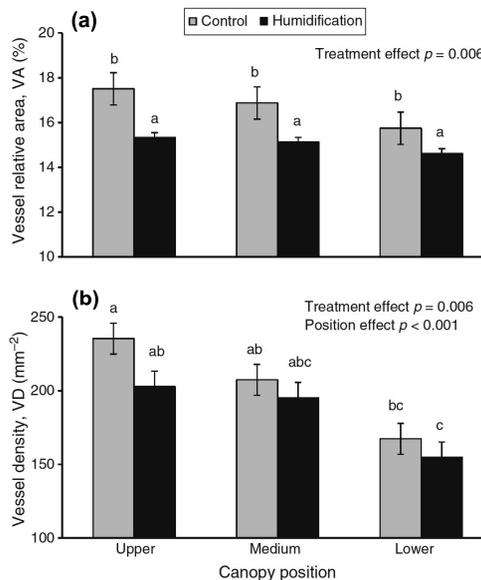


Figure 1. Variation in (a) vessel relative area (VA) and (b) vessel density (VD) in hybrid aspen stemwood with treatment and sample position in control and humidified trees. Error bars indicate \pm S.E. of the means; different letters denote statistically significant ($P < 0.05$) differences.

Table 1. Comparison of xylem characteristics (mean \pm S.E.) in hybrid aspen. Different letters denote statistically significant ($P < 0.05$) differences between the treatments (**xy**) and the sample position (**ab**)

Characteristic	Origin	Control	Humidification
Vessel lumen diameter, D_v (μm)	branch	26.4 \pm 0.6 a	26.4 \pm 0.6 a
	stem	37.3 \pm 0.6 b	36.7 \pm 0.6 b
Vessel lumen area, A_v (μm^2)	branch	630 \pm 30.3 a	632 \pm 30.3 a
	stem	1280 \pm 42.8 b	1229 \pm 42.8 b
Vessel grouping index, V_G	branch	1.67 \pm 0.02 a	1.70 \pm 0.02 a
	stem	1.65 \pm 0.02 a	1.69 \pm 0.02 a
Relative vessel area, VA (%)	branch	13.2 \pm 0.5 a	12.5 \pm 0.5 a
	stem	16.7 \pm 0.42 bx	15.0 \pm 0.4 by
Vessel density, VD (mm^{-2})	branch	273 \pm 12.4 a	273 \pm 12.4 a
	stem	203 \pm 6.0 bx	184 \pm 6.1 by
Xylem vulnerability index, I_{vul}	branch	133 \pm 14.1 a	134 \pm 14.1 a
	stem	260 \pm 9.2 b	264 \pm 9.2 b
Hydraulically weighted mean diameter, D_h (μm)	branch	31.0 \pm 0.8 a	31.0 \pm 0.8 a
	stem	44.7 \pm 0.7 b	43.76 \pm 0.7 b
Theoretical specific conductivity, k_t ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	branch	3.26 \pm 0.3 a	3.18 \pm 0.3 a
	stem	7.05 \pm 0.4 bx	5.73 \pm 0.4 by
Wood density, ρ (g cm^{-3})	branch	0.43 \pm 0.01 a	0.43 \pm 0.01 a
	stem	0.36 \pm 0.01 b	0.37 \pm 0.01 b
Specific hydraulic conductivity, k_S ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	branch	9.57 \pm 1.1 a	9.98 \pm 1.1 a
	stem	33.2 \pm 1.8 bx	40.0 \pm 1.8 by
Branch hydraulic conductance, K_B ($\times 10^{-3} \text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)	branch	1.4 \pm 0.3	1.1 \pm 0.2

VA in hybrid aspen stems was positively correlated with VD ($R^2 = 0.19$, $P = 0.001$). Thus, VA depended more on vessel density (partial correlation coefficient: 0.69–0.71) than on vessel size (D_v , A_v ; partial correlation coefficient: 0.62–0.64). In contrast, for theoretical specific conductivity (k_t), the respective partial correlation coefficients were 0.51–0.55 and 0.84–0.87 (I). These results are consistent with Poorter et al. (2010), who found that the total conductive area of vessels is mostly determined by vessel density, while conductance is mostly determined by vessel diameter, explaining why total vessel cross-sectional area and hydraulic conductance are generally uncoupled. Former studies (Zanne et al. 2010; Hietz et al. 2017) have found that vessel size influences hydraulic conductivity more than the total vessel lumen area.

Increased air humidity influenced not only vessel size but also intervessel pit dimensions (I). In aspen stems, the pit membrane area (A_{pit}) and pit aperture area (A_{ap}) decreased in response to the humidification treatment (Table 2). Previous studies have demonstrated that larger pit membrane areas and larger pit apertures enable higher flow rates and concomitantly higher sapwood hydraulic conductivity (Lens et al. 2011; Jacobsen et al. 2016). Experimentally measured specific hydraulic conductivity (k_s) was negatively correlated with pit density (PD), pit membrane area and pit field fraction (PF), and the Pearson correlation coefficients were -0.27 , -0.29 and -0.36 , respectively (I). Therefore, at first sight, changes in k_s could not be explained by measured pit characteristics, but non-measured pit characteristics may have affected k_s . The hydraulic efficiency of bordered pits is primarily determined by the structure of the pit membrane, including the average porosity and thickness of the membrane (Choat et al. 2008). However, in *Ficus* species, Li et al. (2019) found that the area and diameter of the pit aperture are inversely correlated with sapwood-specific hydraulic conductivity. Sapwood hydraulic conductivity of *Pinus edulis* and *Juniperus monosperma* increased with increasing moisture availability, but this did not influence the diameter of tracheids (Hudson et al. 2018). The authors suggested that the changes in conduction efficiency were caused by changes at the pit structure level.

The humidification treatment had no significant effect on hydraulic and anatomical traits of hybrid aspen branches (I; Table 1). The treatment also had no effect on hydraulically relevant vessel characteristics of hybrid aspen coppice (III) and on hydraulic and anatomical traits in both branches and stems of silver birch (IV). Our results suggest that the wood anatomical structure of *B. pendula* is conservative with respect to the increasing atmospheric humidity predicted for high latitudes in the future, although trees grown in elevated RH demonstrated slightly lower wood densities.

Theoretical specific conductivity (k_t) of hybrid aspen coppice stems was not influenced by the humidity treatment, while the experimentally measured maximum conductivity (k_{max}) decreased in response to elevated RH (III). k_{max} decreased from $4.42 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ in the control to $3.94 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ in the humidification treatment, while the trend was well correlated with increasing wood density. The decrease in k_{max} can be explained by the integrated effect of statistically non-significant slight shifts in several hydraulically relevant anatomical traits (D_h , VA, VD) recorded in aspen wood (Table 3 in III).

Table 2. Comparison of bordered pit characteristics (mean \pm S.E) and results of ANOVA for effects of the humidification treatment and canopy position on pit traits. *ns*, not significant

Characteristic	Control	Humidification	Effect	Significance
Pit area, A_{pit} (μm^2)	58.3 \pm 0.5	56.8 \pm 0.5	Treatment	$P = 0.022$
			Canopy position	$P < 0.001$
Pit aperture area, A_{ap} (μm^2)	6.10 \pm 0.1	5.80 \pm 0.1	Treatment	$P = 0.032$
			Canopy position	$P < 0.001$
Pit density, PD (mm^{-2})	12443 \pm 267	12246 \pm 249	Treatment	<i>ns</i>
			Canopy position	$P < 0.001$
Pitfield fraction, PF (%)	70.6 \pm 2.3	68.3 \pm 1.9	Treatment	<i>ns</i>
			Canopy position	<i>ns</i>

In both studied broadleaved species, trees' growth rate slowed down in response to the long-term exposure to elevated air humidity, and consequently, stem radial increments (**I**), stem diameter or tree height decreased (**III**, **IV**). Hydraulic conductance is commonly positively related to plant growth rates (Tyree 2003; Zhang and Cao 2009). The growth response of our experimental trees varied over time, but across several years, it provides evidence of a stress reaction with respect to increased environmental humidity. Reduced xylem conductivity and larger constraints to foliage water supply are likely one of the reasons contributing to growth retardation (**II**). In fact, disproportionate changes in hydraulic versus stomatal conductance become a detrimental factor in the case of weather extremes, rather than decreased xylem conductivity itself (Sellin et al. 2014). Under high evaporative demand, this begins to limit canopy conductance and may lead to the dysfunction of the hydraulic system. In addition to hydraulic constraints, reduced transpirational flux under elevated air humidity diminishes nutrient movement via mass flow in soil and reduces nutrient uptake and transport to leaves (Tullus et al. 2012; Sellin et al. 2013). Lowered leaf nutritional status causes a decline in photosynthetic capacity, another mechanism that contributes to the slowdown in growth (**II**).

Over time, however, growth reduction diminishes because trees can gradually acclimate to more humid air conditions (Rosenvald et al. 2020; Tullus et al. 2020). Plant growth responses vary depending on the environmental conditions of particular habitats. For example, Nielsen et al. (2017) showed that more summer precipitation in western Greenland promotes the growth rate of *Betula nana*. Higher growth rates are supported by a larger lumen area and higher vessel grouping

(vessel connectivity), which enable ample leaf water supply due to higher hydraulic conductivity.

Xylem resistance to cavitation induced by the air injection method was not affected by humidification treatment in hybrid aspen (Figure 6 in **III**). This is in accordance with I_{vul} , which was also invariant to the humidity treatment (Table 1; Table 4 in **III**). I_{vul} of branches in both studied tree species was significantly lower than that of stems, indicating that branches are more resistant to embolism than trunks (Johnson et al. 2016). Control and humidity-treated trees differed neither by native embolism level.

3.2. Impact on tissue proportions in stems

Increased air humidity influenced the proportions of xylem parenchyma in hybrid aspen stems at the FAHM site (**II**). Stemwood of the trees growing in humidified plots exhibited an increased amount of ray parenchyma, whereas rays were bigger and more numerous (Table 3). The proportion of tangential surface occupied by rays, considered equal to the proportion of parenchyma volume (Gartner et al. 2000; Spicer and Holbrook 2007), increased by 25.7% ($P = 0.005$). Previous studies indicate that both angio- and gymnosperm trees growing in water deficit conditions usually have more abundant ray parenchyma (Esteban et al. 2012; Fonti et al. 2013; Morris et al. 2016; Godfrey et al. 2020). In the case of drought stress, more parenchyma tissue enables the storage of more water and nutrients, especially nonstructural carbohydrates, and due to this, plants have a better ability to survive (Rodríguez-Calcerrada et al. 2015). At the FAHM site, trees with greater parenchyma volume had increased nitrogen concentrations in stemwood (Tullus et al. 2014). An increase in the proportion of living parenchyma as a result of air humidification can also be treated as a stress response, similar to that reported for other stressful environments, such as high elevation or extreme climate (Godfrey et al. 2020). Some conifer species show higher parenchyma fractions in wet and cold environments (Godfrey et al. 2020).

Living parenchyma tissue, compared to dead xylem cells, requires continuously energy, which is used for maintenance respiration. In the case of a large parenchyma fraction, less carbohydrates remain for plant growth (Carey et al. 1997; Maier et al. 1998; Spicer and Holbrook 2007; Rodríguez-Calcerrada et al. 2015). An increased proportion of parenchyma and accompanying high respiration costs are probably one of the reasons why trees grown in high humidity demonstrated certain growth retardation (**II**). Elevated air humidity has a dual effect on trees concerning maintenance respiration. First, larger investments in vascular tissues relative to foliar area cause an increase in the ratio of non-photosynthetic to photosynthetic tissues, leading to higher respiration costs on a relative scale, determined by the volume of sapwood. Second, an increase in the proportion of living parenchyma cells relative to dead xylem elements in sapwood, in turn, enhances respiration costs (Carey et al. 1997; Maier et al. 1998; Spicer and Holbrook 2007). Aritsara et al. (2021) reported that species with higher axial parenchyma fraction

have significantly higher hydraulic conductivity, while species with a high ray parenchyma fraction and high vessel-to-ray connectivity demonstrate lower hydraulic conductivity. Thus, the reduced hydraulic capacity observed in hybrid aspen in response to elevated air humidity may also be associated with changes in stem tissue proportions, i.e. with decreased VD and VA (**I**) and increased amount of ray parenchyma (**II**). Jupa et al. (2019) reported that xylem of ring-porous species contains greater proportions of axial parenchyma, which is probably responsible for greater seasonal ion-mediated changes in hydraulic conductivity compared to diffuse-porous species.

Table 3. Mean values of ray parenchyma traits in stemwood of 1-year-old hybrid aspen coppice. Across all analysed quantitative traits, the increase of parenchyma proportion is highly significant (Hotelling's multivariate T^2 test, $P < 0.001$).

Anatomical trait	Control	Humidification	Change %
Total area of parenchyma rays in tangential view ($\mu\text{m}^2 \text{mm}^{-2}$)	7.88×10^4	9.91×10^4	+25.7 ^a
Parenchyma ray height in tangential view (μm)	115.3	120.5	+4.5
Total parenchyma ray length in tangential view ($\mu\text{m} \text{mm}^{-2}$)	1.23×10^4	1.30×10^4	+5.3
Number of cells in one parenchyma ray in tangential view	6.8	7.1	+4.4
Total area of parenchyma rays in cross-section ($\mu\text{m}^2 \text{mm}^{-2}$)	4.51×10^4	4.75×10^4	+5.1
Number of rays in cross-section (mm^{-2})	23.9	25.3	+5.9
Parenchyma volume index ^b ($\mu\text{m}^3 \text{mm}^{-2}$)	5.19×10^6	5.72×10^6	+10.3

^aStatistically significant effect (ANOVA, $P=0.005$)

^bArea of parenchyma rays in a cross-section multiplied by the mean ray height in the tangential view

Olano et al. (2013) showed that more precipitation in Mediterranean environments during the formation of wood increases jasmonate and ethylene levels and these compounds promote processes targeted at the activation of ray initials. Similar processes are started in the case of flooding (Yamamoto et al. 1987). In the FAHM experiment, trees growing in higher air humidity experienced soil hypoxia and excess water in soil due to reduced transpiration at the beginning of the growing period (Hansen et al. 2013). Ethylene plays a crucial role in adapting plants to hypoxia caused by excess water (Hartman et al. 2021). Under the influence of ethylene, the cambium produces more parenchyma, shorter fibres, and shorter vessels compared to mesic conditions (Junghans et al. 2004). Several studies (Yamamoto et al. 1987; Kozłowski 1997; Rocha et al. 2018) confirm that plants produce more ray parenchyma under flooding conditions.

3.3. Alterations in leaf vascular tissues, stomatal morphology and leaf hydraulic conductance

Leaves represent structurally and functionally plastic organs responding to changes in various environmental conditions (Poorter et al. 2009; Niinemets et al. 2015; Stojnić et al. 2016). Elevated air humidity also influenced xylem anatomy in the leaves of silver birch (**V**). The mean hydraulic diameter of vessels in birch petioles decreased from 19.6 to 16.9 μm ($P = 0.033$) and in midribs from 16.4 to 14.6 μm ($P = 0.026$). Decreased vessel diameters are commonly related to environmental aridity and help plants withstand drought (Blackman et al. 2010; Nardini et al. 2012). Smaller vessels, higher vessel densities and lower hydraulic conductivity in the leaves are usually associated with higher water-use efficiency (Fichot et al. 2009). Coordination between leaf anatomical and physiological traits is stronger in water deficit conditions than in favourable environments (Fichot et al. 2009; Yin et al. 2018; Brunetti et al. 2019), i.e. under conditions of stronger environmental pressure. In the FAHM experiment, the environment was altered in the opposite direction; in humidified plots, the daytime atmospheric vapour pressure deficit (VPD) was decreased by 5–10% (Niglas et al. 2014, 2015). The reduced AED diminishes water flux through the trees, weakening the need for the development of an efficient water transport system, explaining smaller vessel diameters. In addition, high soil water content in spring after snowy winters and during rainy summers may create hypoxic conditions, which have a negative effect on foliar development, influencing the sapwood-to-leaf area ratio (**II**). Former studies (de Souza et al. 2010; Copini et al. 2016; Doffo et al. 2017) have shown that plants grown in flooding conditions have smaller vessels both in leaves and stems. Changes in vessel dimensions in leaf xylem have considerable consequences at the whole-tree level because leaves largely contribute to total plant conductance, representing a major bottleneck in the water transport pathway (Nardini et al. 2003; Sack and Holbrook 2006).

Leaf hydraulics has a significant effect on growth due to the relationship between growth and leaf water potential (Prado and Maurel 2013). Leaf hydraulic conductance impacts the hydration status of the leaf tissues and low tissue water potential limits photosynthesis (Tsuda and Tyree 2000). Leaf size strongly depends on the hydraulic radius of conduits and the xylem area in petioles (Coomes et al. 2008; McCulloh et al. 2009; Gebauer et al. 2016; Gleason et al. 2018). Moreover, even maximum plant height of evergreen angiosperms is positively correlated both with leaf size and vessel size in petioles, midribs and second-order veins (Gleason et al. 2018).

Growing in an environment with increased air humidity reduced hydraulic efficiency of both petioles and laminae in silver birch (**V**). In petioles, the theoretical conductivity of xylem (k_t) decreased from 1.95 to 1.33 $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ($P = 0.033$) in trees grown in humidified plots compared to the control (**V**). The decline in k_t of petioles was caused by the reduced vessel diameter. Despite decreased D_h in the midrib, the decline in their theoretical conductivity was

statistically insignificant. Experimentally measured hydraulic traits corroborated the decline in leaf hydraulic capacity in response to air humidification (Figure 2). As mean D_h decreased by 11% ($P = 0.026$) and the decline in k_t was statistically insignificant in the midrib, while the decline in K_{lb} was far more substantial (~20%, $P = 0.023$) as a result of the manipulation, one can suppose that the leaf extravascular component was also involved in this response. The extravascular pathway imposes higher resistance to water flow than the vascular pathway, therefore leaf hydraulic conductance (K_L) is strongly affected by the outside-xylem compartment (Liu et al. 2019b). Xiong and Nadal (2020) also demonstrated that outside-xylem conductance has a bigger role in determining K_L than xylem conductance. The decline in extravascular conductance in angiosperm species not only has a major effect on K_L , but it can also cause the decline of whole-plant hydraulic conductance (Scoffoni et al. 2017a). Outside-xylem resistance accounts for 11 to 74% of the total leaf hydraulic resistance, depending on species (Sack et al. 2005). As the extravascular component comprises a large part of K_L , small changes in the outside-xylem resistance could induce a substantial change in leaf hydraulic capacity (Johnson et al. 2012).

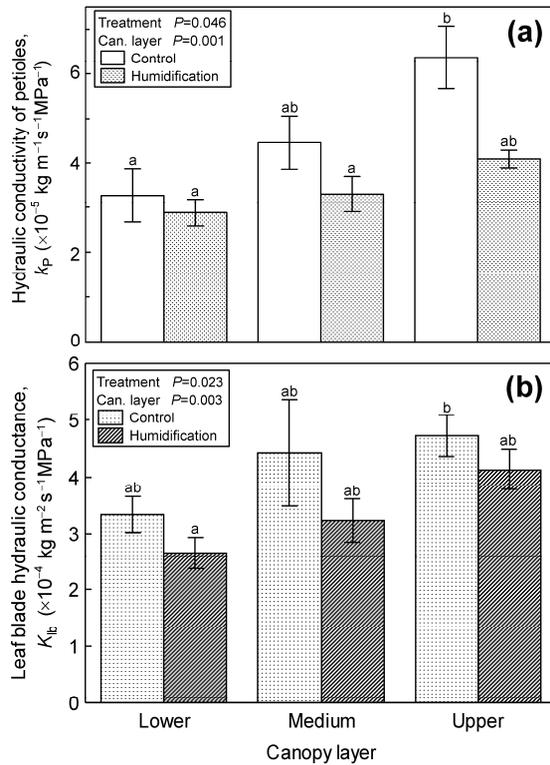


Figure 2. Variation in the hydraulic conductivity of petioles (k_p ; **a**) and hydraulic conductance of the laminae (K_{lb} ; **b**) in silver birch with respect to humidity treatment and canopy position. Error bars indicate \pm S.E. of the means; different letters denote significant ($P < 0.05$) differences between the means

Elevated air humidity had no significant influence on stomatal traits or tissue proportions in silver birch laminae (V). Changes in stomatal size and density in response to higher air humidity are related to leaf expansion and the size of epidermal cells. If leaf expansion does not alter, it is possible that stomatal characteristics also remain unaffected (Hovenden et al. 2012). The formation of bigger stomata with larger pores is considered a universal response to high RH (Fanourakis et al. 2020). In the FAHM experiment, stomatal size did not change, while a reduction in stomatal density and stomatal pore area index (SPI) was observed in the leaves of hybrid aspen developed in increased air humidity (Niglas et al. 2015). Hybrid aspen coppice grown under elevated RH demonstrated a faster stomatal response to changes in atmospheric vapour pressure, but higher sensitivity was not associated with stomatal morphology.

The artificially elevated air humidity did not have significant effects on the leaf structural and functional traits of hybrid aspen saplings (VI). Silver birch and hybrid aspen are both fast-growing and light-demanding hardwoods, but silver birch is a strictly isohydric tree species, while hybrid aspen is inclined to anisohydric behaviour because of its weak stomatal control over water losses accompanied by low leaf water potentials (Aasamaa et al. 2014; Kupper et al. 2018) and a high degree of native embolism (III). Thus, leaf morpho-anatomical and hydraulic traits of isohydric silver birch are more sensitively adjusted with respect to changing environmental conditions compared to anisohydric hybrid aspen.

3.4. Shifts in biomass allocation

Increased air humidity also induced changes in above-ground biomass allocation. In hybrid aspen, the humidification treatment increased the sapwood area-to-leaf area ratio both in coppice (Table 1 in III) and in branches of 6-year-old saplings (Table 1 in I). The most substantial shifts in biomass allocation took place in fast-growing coppice shoots exposed to elevated RH, resulting in a 34% higher ($P < 0.001$) average Huber value (HV) compared to the control. The stem volume-to-leaf area ratio was 15% greater ($P < 0.05$) in plants grown under humidification than in control plants.

In stems and branches of silver birch trees, we observed shifts in HV in the same direction; however, the changes turned out to be statistically insignificant (Table 1 in IV). Previously, Sellin et al. (2013) reported a significant increase in HV in birch stems. Biomass allocation of hybrid aspen in favour of vascular tissues (i.e. increase in HV) can be considered a reaction to compensate for the reduced xylem water-transport efficiency in trees growing under low AED. Higher HV maintains the adequate capacity of stems to transport water to leaves (Carter and White 2009). However, larger investments in vascular tissues relative to photosynthetic tissues cause higher maintenance respiration costs on a relative scale (Ryan 1990). The relative decrease in leaf area also suggests that leaf development in fast-growing deciduous trees is more sensitive to soil hypoxia-induced stress than stem growth (II). Previous studies (Smit et al. 1989; Mielke et al. 2003; Evans et al. 2009) have corroborated that leaf development is inhibited under soil hypoxia.

3.5. Vertical variation of xylem and foliar traits with respect to acclimation to environmental gradients existing within a canopy

The hydraulic efficiency of stemwood decreased in the apical direction in both hybrid aspen (I) and birch trees (IV). The hydraulic diameter of vessels and both theoretical and experimentally measured specific conductivities of the xylem were highest at the stem base (Figure 3; Figures 2 and 6 in I). Vertical variation in stem hydraulic traits enables trees to grow taller, distribute water across the vertical canopy profile and function near their hydraulic limits (Couvreur et al. 2018). It is an important prerequisite for trees, plants of great size, that experience considerable within-canopy environmental gradients to support higher stomatal conductance and transpiration rates in sun-exposed foliage, which is photosynthetically the most important part of the canopy (Sellin et al. 2010). Such a design, based on the distally tapering pattern of xylem conduits, reduces the effect of height on the total path-length resistance and enables adequate water supply to the upper canopy layers (Anfodillo et al. 2013; Olson et al. 2014; Rosell et al. 2017).

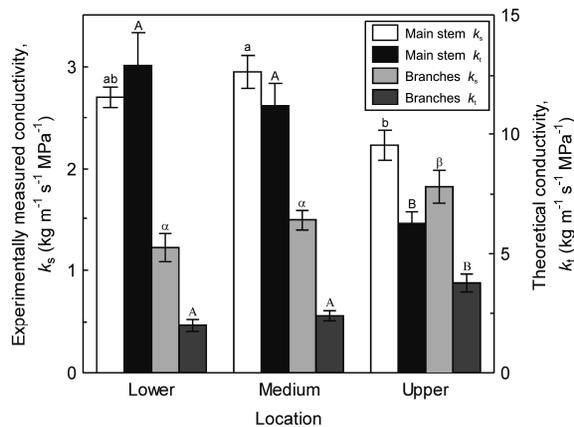


Figure 3. Variation in experimentally measured (k_s) and theoretical hydraulic conductivity (k_t) of xylem at different sample locations in silver birch. Error bars indicate \pm S.E. of the means; different letters denote statistically significant ($P < 0.05$) differences

The hydraulic capacity of hybrid aspen branches tended to be greatest in the mid-canopy (Figure 3 in I), although vessel area (A_v) and Huber value (HV) increased towards the treetop (Table 1 and Figure 6 in I). A medium third of the canopy contained nearly half of the total assimilating surface of young aspen trees (VI), and those leaves need an efficient water conducting system to provide sufficient water delivery. In birch branches, in contrast, the highest values of D_h and VA, as well as the highest k_s and k_t , occurred in the upper canopy layer (Figures 3 and 4 in IV). Lower-canopy branches and shade leaves are less efficient at conducting

water to evaporation sites, imposing constraints on stomatal conductance consistent with their inherently higher water-use efficiency (Sellin et al. 2010).

High irradiance in upper canopy layers exposes leaves to more negative water potentials because of higher evaporative demand in comparison to shady micro-environments; thus, upper-canopy foliage requires more efficient delivery of water to cool the leaves and keep stomata open (Avila et al. 2021). In silver birch (Table 3 in V) and hybrid aspen (Figure 4 in VI), the upper-canopy leaves have petioles and midribs with larger vascular bundle areas, cross-sectional area of the xylem, hydraulically weighted diameter of vessels and vein densities in the lamina. In birch trees, leaf hydraulic efficiency both in petioles and laminae increased acropetally within the crowns (Figure 2; Table 2 in V), supported by spatial trends in relevant anatomical traits (Table 3 in V). In hybrid aspen, leaf hydraulic conductance and petiole conductance tended to be highest in the mid-canopy (Figure 4), although the vascular traits of laminae should favour a leaf-level water supply in the upper canopy (VI). The mean density of minor veins (VLA_{\min}) expressed per unit lamina area increased from 7.8 mm mm^{-2} in the lower canopy to 9.0 mm mm^{-2} in the upper canopy ($P < 0.001$), determining the vertical trend ($P = 0.005$) in total vein density (VLA) in the same direction. K_{lb} was numerically lowest in the upper crown thirds, although it did not differ significantly from that of the lower canopy layers. Top leaves of hybrid aspen were thicker, and the increase of vein density was too small to compensate for the longer extravascular pathway, resulting in a decreasing trend in lamina hydraulic conductance, which in turn affected K_L . In fact, both the major and minor vein densities expressed per unit lamina volume (VLV) decreased upward (Figure 4F in VI).

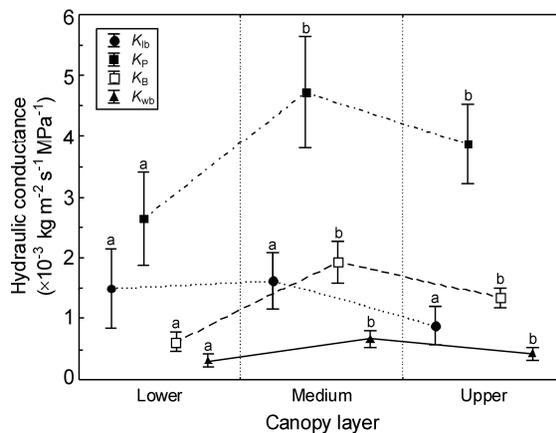


Figure 4. Mean (\pm S.E.) leaf and branch hydraulic conductance (K_{lb} —leaf laminae, K_p —petioles, K_B —bare branch, K_{wb} —whole branch) in different canopy layers of young hybrid aspen trees. Different letters denote significant ($P < 0.05$) differences between the canopy layers.

The dimensions of stomata decreased, while stomatal density increased upward in hybrid aspen crowns (Figure 5). These opposite trends translated to a relatively uniform stomatal pore area index (SPI) and maximum stomatal conductance (g_{Smax}) across the canopy vertical profile. No evidence was found for structural/functional coordination between leaf hydraulic function and stomatal characteristics in aspen saplings, which can be explained by the near-anisohydric behaviour of the species (VI). Because of weak stomatal control over water losses, SPI and g_{Smax} can be spatially adjusted roughly evenly and functional differentiation of stomata with respect to intracanopy environmental heterogeneity is not pronounced. Flexible stomatal development and their strict regulation is probably not necessary in fast-growing young aspen trees under ample soil water supply; on the contrary, these traits may restrict their carbon gain and growth rate. Our findings are consistent with Smith et al. (2011), who indicated that the youngest age classes (<10 years) of *Populus tremuloides*, one of the parent species of hybrid aspen, exhibit the highest stomatal conductance and lowest WUE. At adequate water supply, stomatal conductance, transpiration and growth rates are higher in anisohydric *Populus* species than isohydric ones (Attia et al. 2015). Under water stress, anisohydric species have higher photosynthetic rates, while WUE is higher in isohydric poplars.

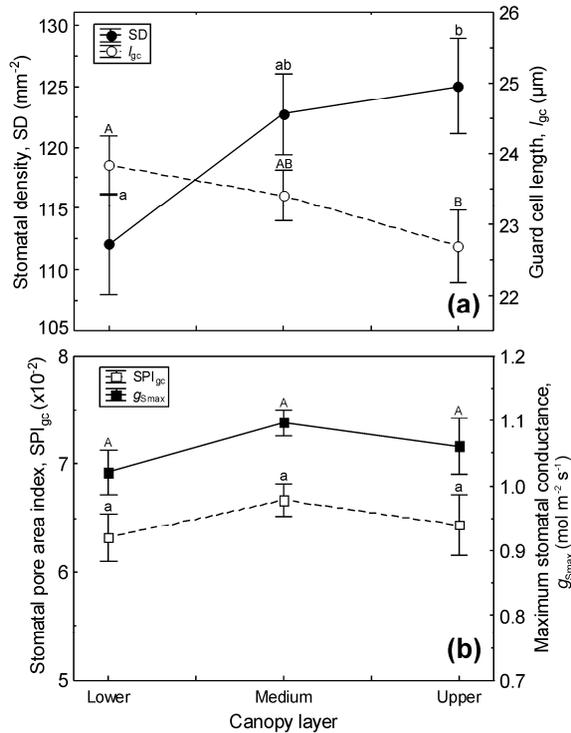


Figure 5. Vertical trends in stomatal traits (mean \pm SE) within crowns of hybrid aspen: **(a)** stomatal density (SD) and guard cell length (l_{gc}); **(b)** stomatal pore area index (SPI_{gc}) and maximum stomatal conductance (g_{Smax}). Different letters denote significant ($P < 0.05$) differences between the canopy layers.

Within the crown of silver birch, both stomatal dimensions and stomatal density demonstrated increasing trends in the apical direction (Figure 6; Table 3 in V) with increasing irradiance and AED. Higher stomatal density and bigger stomata combined provide a higher stomatal conductance, which requires more developed vascular tissues to support the consequent transpirational water fluxes in leaves. Thus, both SPI and K_{lb} increased in the direction of the treetop in *B. pendula*, a strictly isohydric tree species (V). Stomatal traits of birch were positively correlated with several petiole and leaf midrib vascular traits, as well as with venation density, demonstrating a coordinated adjustment of vascular and hydraulic traits in accord with environmental gradients existing in forest canopies.

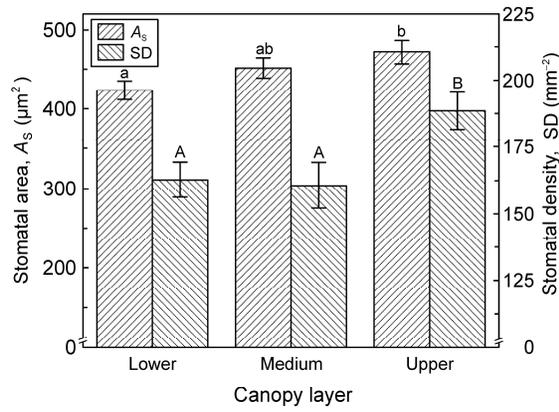


Figure 6. Variation in stomatal area (A_s) and stomatal density (SD) with canopy position in silver birch. Error bars indicate \pm S.E. of the means; different letters denote statistically significant ($P < 0.05$) differences between the canopy layers.

In both species, branchwood consisted of substantially smaller vessels than stemwood (Table 1; Table 2 in IV). Leaf vascular bundles, in turn, contained smaller vessels than branches. All vascular traits (size of vascular bundles, xylem area, diameter of vessels, k_t) were larger in petioles compared to the midribs (silver birch: Tables 3 and S1 in V; hybrid aspen: Table S1 in VI). These results are in accordance with previous findings that vessel diameter increases with distance from the stem tip (Soriano et al. 2020). The hydraulic diameter of xylem conduits in angiosperm leaves increases along the midrib from the leaf tip to the petiol (Lechthaler et al. 2020). The narrowest vessels are located in veins of higher orders, where water exits the xylem into the mesophyll (Olson et al. 2021). Tip-to-base xylem conduit widening is a universal trend, which is valid for species from different climate conditions and occurs independently of tree height and leaf size (Fajardo et al. 2019; Olson et al. 2021). The distally tapering pattern of xylem conduits is considered a strategy that reduces the effect of height on total path length resistance and minimises the tree-level hydrodynamic resistance of water

transport from roots to leaves (Bettiati et al. 2012; Anfodillo et al. 2013). Rapid widening from tip to base helps to minimize hydraulic resistance, while slower conduit widening minimizes carbon cost and embolism risk, indicating that carbon economy is also an important factor affecting the plant water-conducting system (Koçillari et al. 2021).

4. CONCLUSIONS

The main conclusions of this thesis are as follows:

1. Increasing air humidity causes changes in the anatomical structure of stems and leaves in broadleaved trees that leads to a lower hydraulic efficiency of their water transport system, proving the first hypothesis. Reduced hydraulic efficiency of xylem and leaf extravascular pathway imposes bigger constraints on foliage gas exchange and may limit the growth rate under high atmospheric evaporative demand.
2. Elevated air humidity caused changes in biomass allocation in favour of vascular tissues, which can be treated as a mechanism compensating for the reduced hydraulic efficiency of stem xylem. It is also possible that leaf development is more sensitive to soil hypoxia, concomitant with diminished transpirational fluxes, compared to the xylem. Larger investments in stem xylem in relation to foliage cause an increase in the ratio of non-photosynthetic to photosynthetic tissues, leading to larger maintenance respiration costs determined by the volume of parenchyma.
3. Trees of hybrid aspen grown in ambient conditions and under elevated air humidity did not differ in the native embolism level and susceptibility to artificially induced cavitation. Thus, the functional vulnerability of stemwood does not represent a potential threat to hybrid aspen in light of long-term regional climate trends. The hypothesis that elevated relative humidity induces alterations in the structure of xylem cells and stomata that increase cavitation risk was not supported.
4. High air humidity affects not only investments in xylem tissue but also the differentiation of wood cells, increasing the share of ray parenchyma in hybrid aspen stems. Our results corroborate the third hypothesis concerning the effect on tissue proportions in xylem. An increase in the proportion of living parenchyma cells in relation to dead xylem elements in sapwood additionally enhances respiration costs, leaving less resources to sustain growth processes.
5. Both studied tree species—silver birch and hybrid aspen—are fast-growing and light-demanding hardwoods, but they differ in water-use strategies. Anisohydric or isohydric species respond differently to environmental gradients, reflecting in trees' anatomical structure. Leaf morpho-anatomical and hydraulic traits of isohydric silver birch are more sensitive to changing environmental conditions compared to anisohydric hybrid aspen. No evidence of coordination between leaf hydraulic function and stomatal characteristics was observed in young hybrid aspen stands, which contrasts with that in silver birch.
6. Despite some slight changes in xylem traits, the wood anatomical structure of the studied broadleaved tree species is generally conservative with respect to climate trends, including increasing atmospheric humidity predicted for high latitudes. On a longer time scale, the effects on plant hydraulics may even diminish because trees can gradually acclimate to more humid air conditions.

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SUMMARY IN ESTONIAN

Suurenenud õhuniiskuse mõju heitlehiste puude veetransporditeede ehitusele

Vesi on taimedele eluliselt oluline faktor, mis teeb võimalikuks fotosünteesi toimumise, kasvu ja ellujäämise. Vesi liigub puudes transpiratsiooni poolt süsteemis muld-juur-leht tekitatud veepotentsiaalide gradiendi tõttu. Transpiratsiooni käivitajaks on veekaod lehestiku pinnalt ja selle intensiivsust reguleeritakse eelkõige õhulõhede avatusega. Vesi liigub mullast juurte, tüve ja okste kaudu puulehtedesse mööda juhtkudet – ksüleemi, mille koosseisu kuuluvad trahheed ja trahheiidid moodustavad suurima osa taimesisisest veetranspordi teekonnast. Puude veejuhtivus ja kavitatsioonikindlus on eelkõige määratud ksüleemi ehitusega. Kavitatsioon on pideva veesamba katkemine juhtelemendis muutunud hüdrostaatilise rõhu tõttu ja mille tagajärjel täitub juhtelement õhuga. Kaviteerunud trahheed vähendavad ksüleemi hüdraulilist juhtivust, mis lõppkokkuvõttes limiteerib lehtede veevarustust. Kavitatsiooni poolt põhjustatud hüdraulilise juhtivuse oluline langus tüves, lehtedes või juurtes võib põhjustada õhulõhede sulgumist. Suured trahheed ja trahheiidid on suurema veejuhtimisvõimega. Väike muutus ksüleemielemendi raadiuses põhjustab suure muutuse selle veejuhtimisvõimes, sest vastavalt Hagen-Poiseuille' seadusele on kapillaari hüdrauliline juhtivus võrdeline tema raadiuse neljanda astmega. Taimed on dilemma ees – suurema läbimõõduga juhtelemendid tagavad kõrgema hüdraulilise juhtivuse, teisalt aga väheneb muutilikus keskkonnas sellise ehituse korral ksüleemi kavitatsioonikindlus. Peale selle mõjutavad hüdraulilist juhtivust juhtelementide pikkus, rakukestade omadused, perforatsiooniplaatide olemasolu, aga ka juhtelementide tihedus ja arv ning koobaspooride ehitus elementide vahel. Lisaks on veevoogude regulatsioonil taimes oluline roll ka õhulõhede morfoloogial, mis määrab õhulõhede juhtivuse.

Erinevad keskkonnafaktorid nagu valguse, vee ja toitainete kättesaadavuse muutused mõjutavad veetransporditee ehitust ja seeläbi ka selle veejuhtivust. Põuaga seostatakse väiksema läbimõõduga trahheesid, mis on madalama hüdraulilise juhtivusega, kuid samas kavitatsioonikindlamad. Muutuste kohta, mis on põhjustatud suurenenud vee kättesaadavusest, on vähem informatsiooni ja andmed vastuolulisemad. Põhja-Euroopale ennustatakse käesoleva sajandi jooksul sademete hulga suurenemist, veelgi tõenäolisemalt sademete sageduse suurenemist, mõlemaga kaasneb atmosfääri suhtelise õhuniiskuse tõus lokaalsel või regionaalsel tasandil. Suurenenud õhuniiskus, võib kaasa tuua muutusi nii puude veetransporditeede anatoomilistes kui ka funktsionaalsetes tunnustes.

Minu doktoritöö eesmärgiks oli testida järgmisi hüpoteese:

- 1) Suurenev suhteline õhuniiskus indutseerib ksüleemi ehituses muutusi, mis põhjustavad madalamat tüve ja lehtede hüdraulilist efektiivsust.

- 2) Suurenev suhteline õhuniiskus kutsub ksüleemi rakkude ja õhulõhede ehituses esile muutusi, mis suurendavad kavitatsiooniriski, muutes taimed haavatavamaks ekstreemsete ilmastikutingimuste suhtes (kestev põud, kuumalained).
- 3) Õhuniiskuse edasine tõus mõõdukalt niiskes Eesti kliimas muudab maltspuidus erinevate kudede proportsioone – suureneb parenhüümi osatähtsus.

Suureneva õhuniiskuse mõjude uurimiseks metsa ökosüsteemi funktsioneerimisele on Tartumaal Kastre vallas loodud Metsaökosüsteemi õhuniiskusega manipuleerimise (*Free Air Humidity Manipulation*, FAHM) katseala, kust koguti andmed käesoleva doktoritöö jaoks. FAHMi katsealal uuriti kahte lehtpuuliiki – hübriidhaava (*Populus tremula* L. × *P. tremuloides* Michx.) ja arukaske (*Betula pendula* Roth). Samadel katsepuudel, millelt koguti doktoritöö jaoks anatoomia-proove, teostati paralleelselt detailsed hüdraulika mõõtmised.

Suurenenud õhuniiskuses kasvanud hübriidhaabade tüvepuidus oli trahheede tihedus väiksem nagu ka trahheede suhteline pindala. Samuti olid trahheede vaheliste koobaspooride mõõtmed väiksemad kui kontrolltingimustes kasvanud puudel. Niisutustöötlus ei mõjutanud oluliselt trahheede ehitust arukase tüves ja okstes, kuid lehe keskroos ja leherootsus oli trahheede hüdrauliline diameeter suurenenud õhuniiskuse korral väiksem kui kontrollis. Kõik need muutused viitavad sellele, et suurenenud õhuniiskus põhjustab ksüleemi madalamat hüdraulilist efektiivsust. Niisutustöötluses kasvanud puudes on transpiratsioonivoog nõrgem ja seetõttu ei teki keskkonna survet niivõrd efektiivse veetranspordisüsteemi väljakujunemiseks. Suurenenud õhuniiskuse tõttu vähenes arukase leherootsu ja lehelaba hüdrauliline efektiivsus. Leherootsus vähenes hüdrauliline juhtivus trahheede väiksema diameetri tõttu. Hoolimata trahheede vähenenud diameetrist ka keskroos, oli lehelaba hüdraulilise juhtivuse langus põhjustatud rohkem väljaspool ksüleemi kulgeva (s.o. ekstravaskulaarse) transporditee muutustest. Lehe hüdraulilisel võimekusel on oluline tähendus taimel kui terviku jaoks, sest lehtedes on lokaliseeritud suur osa veetransporditee kogu takistusest, lisaks toimub lehtedes fotosüntees, mis vajab pidevat veega varustamist, et säilitada õhulõhede avatus ja vältida kudede dehüdratatsiooni. Maksimaalne hüdrauliline juhtivus ksüleemi veega küllastatuse korral vähenes ka hübriidhaava kännuvõsudes. Kahanenud hüdrauliline efektiivsus võib osutada üheks puude kasvu pidurdavaks teguriks. Aeglustunud transpiratsioonivoo tõttu väheneb toitainete omastamine mullast ja transport lehte, mis põhjustab fotosünteesivõime languse ja kasvu pidurdumise. Eelnevalt kirjeldatud tulemused toetavad esimest hüpoteesi. Samas leiti doktoritöös, et hoolimata väikestest muutustest ksüleemi anatoomias, on uuritud lehtpuuliikide puudu ehitus keskkonna muutuste, s.h. kliimamuutuste suhtes, suhteliselt konservatiivne.

Suurenenud õhuniiskus ei kutsunud ei kase ega hübriidhaava õhulõhede morfoloogias esile olulisi muutusi. Suurenenud õhuniiskusel ei olnud mõju ka ksüleemi kavitatsioonikindlust iseloomustavatele parameetritele hübriidhaava tüvedes ega kännuvõsudes. Seega ei kujuta regionaalsed kliimatrendid puude veejuhtesüsteemi funktsionaalse stabiilsuse vaates hübriidhaava puistutele tulevikus ohtu, mistõttu teine doktoritöös püstitatud hüpotees ei leidnud kinnitust.

Puude reaktsioon suurenevale õhuniiskusele sõltub liikide veekasutuse strateegiast. Arukask ja hübriidhaab on mõlemad kiirekasvulised ja valgusnõudlikud liigid, kuid nad erinevad veekasutuse strateegia poolest. Arukaske iseloomustab rangelt isohüdriline käitumine, mis väljendub selles, et tal on tugev õhulõhede kontroll veekadude üle ja lehe veepotentsiaali hoitakse kindlates piirides. Samas hübriidhaava iseloomustab kalduvus anisohüdrilise strateegia poole – nõrk õhulõhede kontroll, tema veepotentsiaalid langevad madalale ja esineb kõrge looduslik kavitatsiooni tase. Arukasel olid lehe hüdraulilised omadused ja õhulõhede tunnused omavahel tihedalt koordineeritud, kuid hübriidhaaval vastavaid seoseid ei leitud. Lehe morfo-anatoomilised ja hüdraulilised omadused reageerisid isohüdrilisel arukasel keskkonnatingimuste muutumise suhtes oluliselt tundlikumalt võrreldes anisohüdrilise hübriidhaavaga.

Kolmas doktoritöös püstitatud hüpotees kudede proportsioonide muutumise kohta maltspuidus kõrgeenenud õhuniiskuse mõjul leidis kinnitust. Niisutus-töötles kasvanud hübriidhaabadel suurenes tüves 25.7% radiaalsete säskiirte ruumala. FAHMi katse niisutusringides on vähenenud atmosfääri evaporatiivse nõudluse tõttu mulla veesisaldus kõrgem ning kevadeti ja suvel kestvate vihmade tagajärjel võib mullas kujuneda hapnikuvaegus, mis mõjutab ksülogeneesi. Liigniisketes tingimustes kasvanud taimed produtseerivad rohkem taimehormoon etüleenit, mille mõjul toodab kambium rohkem parenhüümi. Erinevalt surnud ksüleemirakkudest kasutab elus põhikude energiat säilitushingamiseks ja vähem ressursse jääb üle kasvaks. Kudede proportsiooni muutumine võib vähendada hübriidhaava puidu hüdraulilist efektiivsust. Suurenenud õhuniiskus mõjutab ka puudesisest biomassi jaotust: suureneb biomassi allokatsioon juhtkudedesse lehestiku suhtes. See nihutab fotosünteesivate ja mittefotosünteesivate kudede suhet viimaste kasuks, mis tähendab hingamiskulutuste suurenemist suhtelises skaalas. Täheldatud allokatsiooni muutuste taga võivad olla erinevad mehhanismid: vähenenud puidu tiheduse ja mehhaanilise tugevuse kompenseerimine suurema ressurside paigutusega tüvesse (arukask), vähenenud hüdraulilise efektiivsuse kompenseerimine (hübriidhaab), lehestiku arengu suurem pidurdumine võrreldes tüve juurdekasvuga kõrge suhtelise õhuniiskuse ja mulla hüpoksia mõjul (mõlemad liigid).

Puud on pikaajalised organismid ja muutused metsaökosüsteemides toimuvad suure ajalise viibega. Seetõttu on vajalik samasuunaliste uuringutega jätkata, tegemaks usaldusväärseid järeldusi kliimamuutuste mõjude kohta metsaökosüsteemidele pikemas ajaskaalas, sest uuritud lehtpuuliigid on võimelised kohanema niiskemate tingimustega. Seda kinnitavad meie uurimiserühma poolt saadud uuringutulemused, mis näitavad et puude kasvu aeglustumine aja jooksul väheneb.

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