

ANNIKA JOY MEITERN

Impact of potassium ion content
of xylem sap and of light conditions
on the hydraulic properties of trees



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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** **Meitern A.**, Õunapuu-Pikas E., Sellin A. 2017. Circadian patterns of xylem sap properties and their covariation with plant hydraulic traits in hybrid aspen. *Journal of Plant Physiology* **213**: 148–156.
- II** Sellin A., Niglas A., Õunapuu E. & **Karusion A.** 2013. Impact of phloem girdling on leaf gas exchange and hydraulic conductance in hybrid aspen. *Biologia Plantarum* **57**: 531–539.
- III** Sellin A., Sack L., Õunapuu E., **Karusion A.** 2011. Impact of light quality on leaf and shoot hydraulic properties: a case study in silver birch (*Betula pendula*). *Plant, Cell & Environment* **34**: 1079–1087.
- IV** Sellin A., Õunapuu E., **Karusion A.** 2010. Experimental evidence supporting the concept of light-mediated modulation of stem hydraulic conductance. *Tree Physiology* **30**: 1528–1535.

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The participation of the author in preparing the listed publications is as follows:

- Paper I collection and analysis of the data and lead author in writing the paper
- Paper II collection of the data and participation in writing the paper
- Paper III collection and analysis of the data and participation in writing the paper
- Paper IV collection and analysis of the data and participation in writing the paper

LIST OF ABBREVIATIONS

AED	atmospheric evaporative demand
A_L	leaf area (m^2)
A_X	cross-sectional area of the xylem (m^2)
AQP	aquaporin
BSC	bundle-sheath cell
E	transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$)
FAHM	Free Air Humidity Manipulation experiment
Fl	number of flushes
g_s	stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
H_{Brel}	relative branch height
HV	Huber value ($\text{m}^2 \text{m}^{-2}$)
H_T	tree height (m)
k	specific hydraulic conductivity of xylem ($\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)
K_B	hydraulic conductance of leafless branch ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
k_{bw}	specific conductivity of branch-wood ($\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)
K_{in}	initial hydraulic conductance of the embolised stem segment ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_L	leaf hydraulic conductance ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_{lb}	hydraulic conductance of leaf blade ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
k_{max}	maximum hydraulic conductivity of xylem ($\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)
K_P	petiole hydraulic conductance ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_S	hydraulic conductance of shoot ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_{sat}	maximum hydraulic conductance at full saturation ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_{seg}	hydraulic conductance of the branch segment ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
K_{wb}	whole-plant hydraulic conductance or total hydraulic conductance of soil-to-leaf pathway ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
$[\text{K}^+]$	potassium ion concentration (ppm)
l	length of specimen (m)
NSC	non-structural carbohydrate content
Osm	osmolality (mmol kg^{-1})
pH	acidity of aqueous solution
PLC	percent loss of conductivity (%)
P_N	net photosynthetic rate ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)
PPFD	photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
RH	air relative humidity (%)
T_A	air temperature ($^{\circ}\text{C}$)
T_L	leaf temperature ($^{\circ}\text{C}$)
VAC	vascular associated cells

VPD	atmospheric water vapour pressure deficit (kPa)
$\Delta\Psi$	water potential difference, a driving force for water flow in plants (MPa)
σ_{sap}	electrical conductivity of xylem sap (mS cm^{-1})
Ψ_{B}	branch water potential (MPa)
Ψ_{L}	bulk leaf water potential (MPa)
Ψ_{S}	soil water potential (MPa)

1. INTRODUCTION

1.1. Ecophysiological significance of xylem hydraulic efficiency

Ecophysiology is a science exploring interactions between environments and the functioning of organisms (Leclerc, 2003). Plants are sessile organisms, they cannot move towards needed resources. Hence, light, water, and nutrient availability, and water transport capacity are essentials for their lives (Nardini et al., 2011b; Fitter & Hay, 2012). As all living organisms, plants have to cope with inter- and intra-specific competition (Goldberg & Barton, 1992; Callaway & Walker, 1997) and adapt to continually changing environmental conditions (Jump & Peñuelas, 2005). Capability to adapt to climate change and environmental heterogeneity determines plant populations' ability to survive and to be successful in competition (Jump & Peñuelas, 2005; Parmesan, 2006).

People have been fascinated by the question of how water can get to the top of tall trees and vines (Kirkham, 2014). How can water move in trees over long distances against gravity? Plants can be treated as hydraulic systems comparable with dams and irrigation systems for crops or the blood circulation system of animals. They consist of the same basic elements, like a driving force, pipes, reservoirs, and regulative systems. Pipes in plants are formed from conduits of conducting tissues – vessels and tracheid in the xylem and sieve tubes in the phloem. The energy for water transfer from roots to leaves comes from solar radiation, fuelling through evaporation the transpirational flux, thus generating the driving force (Cruiziat et al., 2002). Water flow through the plant can be treated as an Ohm's law analogy (Tyree & Ewers, 1991), complemented with the cohesion-tension theory that has become the most broadly acknowledged explanation of how water can ascend in plants (Meinzer et al., 2001; Kirkham, 2014; Konrad et al., 2019). According to the cohesion-tension theory, water moves from roots to leaves through the xylem in continuous water columns under tension. This is a passive process driven by the solar-energy-induced water potential differences between roots and leaves (Hacke & Sperry, 2001; Meinzer et al., 2001; Cruiziat et al., 2002; Lucas et al., 2013; Schenk, 2018). Along this way, stem hydraulic traits are adjusted to the height above the ground. This vertical variation in stem hydraulic traits allows tall trees to operate near their hydraulic limits when evaporation is close to a critical limit (Couvreur et al., 2018).

Numerous environmental factors affect plant hydraulic properties (Cochard et al., 2000b, 2007; Brodribb & Holbrook, 2004; Sellin & Kupper, 2007; Öuna-puu & Sellin, 2013; Nardini et al., 2021). Furthermore, hydraulic traits intermediate how plants interact with their abiotic and biotic environments (Sack et al., 2016). The plant vascular system's main essential functions are the delivery of different resources like water, mineral nutrients, sugars, and amino acids to all plant organs (Lucas et al., 2013). Therefore, the structure of the water transport system places physical limits on plant functioning (Ryan et al., 2006; Brodribb,

2009). Water transport efficiency throughout the plant determines gas exchange, photosynthetic rate, growth, tree height, and productivity (Tyree & Ewers, 1991; Brodribb, 2009; Sack et al., 2016; Landsberg et al., 2017). The water transport system has to be efficient enough to keep up photosynthesis, the process that is the basis of plant life (Lambers et al., 2008; Brodersen et al., 2019). More than 90% of the water taken up by a plant is lost in transpiration, while CO₂ is being taken up through the stomata (Kramer & Boyer, 1995). In exchange for a molecule of CO₂, plants lose over 400 H₂O molecules (Bouda et al., 2019). Globally, 62 000 km³ of water flows annually through the water transport pathways inside plants. That makes 80–90% of terrestrial evapotranspiration, and thus plants directly influence our climate (Jasechko et al., 2013). Plant hydraulics impacts plant responses to climate, and species distribution, and ecosystem functioning (Sack et al., 2016). At the same time, tree stems cannot be considered simply as a pathway for water transport. They also act as storage compartments for water and nutrients (Tyree & Ewers, 1991; Meinzer et al., 2001). Water storage capacity is also vital for plants because it regulates the ability to support photosynthesis and growth despite temporary water shortages (Tyree & Ewers, 1991; Cruiziat et al., 2002; Landsberg et al., 2017). Water stored in the stems of large trees may deliver up to 20–30% of daily sap flow (Landsberg et al., 2017). That makes plants able to colonize many various habitats.

1.2. The anatomical structure – a primary factor determining the hydraulic conductivity of xylem

Water moves from the roots to the leaves through xylem conduits down a water potential gradient. There are two main types of conduits in the xylem – vessels and tracheids, consisting of more or less elongated cells with lignified thick secondary walls. Both of them represent dead cells at maturity (Evert, 2006; Schenk, 2018). Conduit cell wall rigidity and strength are essential to avoid a collapse in the presence of strong tensions (Hacke & Sperry, 2001; Lucas et al., 2013). Their diameters vary from 5 µm in conifer needles to >500 µm in the stems of tropical lianas. Their length varies even more – it ranges from a couple of millimetres in tracheids to several metres in vessels (Kramer & Boyer, 1995; Hacke & Sperry, 2001; Brodersen et al., 2019). In vines and ring-porous trees, vessels may be more than 10 m long (Hacke & Sperry, 2001), while tracheids are up to 5 mm long and 8–80 µm in diameter (Kramer & Boyer, 1995; Brodersen et al., 2019). Vessels with larger diameters tend to be longer than narrow vessels (Jacobsen et al., 2019). Tracheids are imperforate tracheary elements typical for gymnosperms, especially conifers, but also common in many other plant families (Evert, 2006; Brodersen et al., 2019). Tracheids are separate cells, while vessels consist of many individual cells, the vessel elements, whose end walls are partly or entirely dissolved during the late stages of cell maturation (Tyree & Zimmermann, 2013).

In addition to the tracheary elements, there are living parenchyma cells in sapwood, whose primary function is storage and biomechanical support (Evert, 2006; Schenk, 2018). Parenchyma rays are also connection bridges between phloem and xylem because they permit the movement of water and solutes laterally between phloem and xylem (De Boer & Volkov, 2003; Spicer, 2014). There is a positive correlation between vessel diameter and volume of axial parenchyma (Morris et al., 2018).

According to the Hagen-Poiseuille law, liquid flow rate is proportional to the fourth power of capillary radius (Tyree & Ewers, 1991; Holbrook & Zwieniecki, 2011; Tyree & Zimmermann, 2013; Bouda et al., 2019). This means that a small increase in vessel diameter causes a substantial increase in its hydraulic conductivity. Therefore, wide vessels are much more efficient water conductors than narrow ones (Cruziat et al., 2002; Evert, 2006; Tyree & Zimmermann, 2013). Extremely wide and long vessels in lianas compensate for the small conducting area in their narrow stems (Tyree & Ewers, 1991). Vessels are more effective water transporters than tracheids because of their greater dimensions (Sperry et al., 2006). Theoretical predictions of flow rate based on vessel diameters may not be correct. In fact, the contribution of wide vessels to sap flow may be much lower because the vessel network is not homogeneous. In a heterogeneous vessel network, transverse pressure gradients arise, which transmit flow from wide to narrow vessels (Bouda et al., 2019). Bouda et al. (2019) showed a considerable rise in transverse pressure gradients in grapevines and a decrease in the wide vessels' contribution to sap flow by 15% of the total.

The hydraulic efficiency of the plant water transport system depends on the conductivity of both conduit lumina and inter-conduit connections (Nijse et al., 2001; Bouda et al., 2019). Separate vessels are interconnected through perforation areas where they lack primary and secondary walls (Evert, 2006). Conduit interconnection areas are bottlenecks that decrease xylem hydraulic conductivity (De Boer & Volkov, 2003; Sperry et al., 2006; Choat & Pittermann, 2009). Therefore, measured conductivity is commonly less than the theoretical conductivity predicted by the Hagen-Poiseuille law (Tyree & Ewers, 1991; Bouda et al., 2019). The nano-porous primary cell walls and pit membranes located in bordered pits between conduits are crucial for water movement efficiency. In order to move from one conduit to the next, water must pass through those high-resistance pit membranes (Hacke & Sperry, 2001; Choat & Pittermann, 2009). Pits allow water to pass between functional conduits, but, at the same time, they prevent air from leaking into the conduit system (Hacke & Sperry, 2001; De Boer & Volkov, 2003). Pit membranes are classically seen as microfiber networks with discrete holes, since porous structures are covered with pectins (Choat & Pittermann, 2009; Lee et al., 2012). Pectins form hydrogel, reacting to solute changes in the surrounding environment and influencing water movement in vessels (Holbrook & Zwieniecki, 2011; Lee et al., 2012). The total area of pits, their shape, and pattern of lignification vary widely among plant species (De Boer & Volkov, 2003). Most of the pits are circular, but only a few of them are of perfectly circular shape (Zhao et al., 2019). New modeling work (Li et al., 2020) suggests that obstructions in

the flow pathway of pit membranes play a more important role in determining flow rate than pore size does.

Conifers generally exhibit higher resistance to water movement because of their short and narrow tracheids, which are less efficient conductors than vessels (Kramer & Boyer, 1995; Choat & Pittermann, 2009). Their bordered pits have a unique structure – in the middle is a dense thickening called a torus surrounded by a thin network-like part, a magro – which determines their hydraulic safety and efficiency (Pittermann et al., 2005; Evert, 2006; Choat & Pittermann, 2009; Losso et al., 2018). Conifers compensate their narrow tracheids with those torus-magro pits because their margo is much more conductive (has less flow resistance) than the homogeneous pit membranes in angiosperm vessels (Pittermann et al., 2005; Sperry et al., 2006; Choat & Pittermann, 2009).

1.3. Water conducting system in changing environment

Xylem anatomy is affected by various environmental conditions, including climate factors (Baas & Wheeler, 2011; Kardošová et al., 2020; Pacheco et al., 2020), especially during the active growth phase (Corcuera et al., 2004; Grill et al., 2004; de Oliveira et al., 2018). For example, drought decreases the diameter of vessels in roots and shoots (Vasellati et al., 2001; Corcuera et al., 2004). Increased air humidity decreases vessel density and vessel lumen diameter in trees growing in mesic forests at high latitudes (Jasińska et al., 2015; Alber et al., 2019). Plants in high-humidity environments tend to have less developed conducting tissues (Sellin et al., 2019), although wood anatomy is rather conservative and not much influenced by air humidity (Alber et al., 2019). Environmental factors alter the partitioning of hydraulic resistance between the vascular and extra-vascular compartments in the leaves, influencing in this way the water transport capacity of leaves (Sack & Holbrook, 2006; Holbrook & Zwieniecki, 2011).

Light availability is one of the relevant environmental factors. Spectral distribution of solar radiation affects plant development and physiological processes in many different ways (Fitter & Hay, 2012). Plant sensitivity to light quality is of great ecological significance, enabling plant acclimation to the spatially heterogeneous and temporally changeable radiation field existing in natural plant communities. Blue light advances spring bud burst (Brelsford & Robson, 2018) and increases chlorophyll content per leaf area, net photosynthetic rate, and stomatal conductance (Hernández & Kubota, 2016); blue and green light also enhance hydraulic conductance (Voicu et al., 2008). Irradiance and the plant's internal circadian clock drive leaf hydraulic conductance (K_L) on a diurnal scale (Bucci et al., 2003; Nardini et al., 2005; Voicu et al., 2008; Johnson et al., 2009, 2011). Long-term shade and sun-exposed conditions shape the anatomy and physiology of the plant's vascular system to a large extent (Fitter & Hay, 2012). Hydraulic conductance is higher in sun-exposed leaves compared to shade leaves (Sack et al., 2003; Sellin & Kupper, 2007; Sellin et al., 2013). This is crucial because

the sun leaves of tall trees are more exposed to irradiance and face greater water and temperature stresses than shade leaves (Fitter & Hay, 2012).

Temperature generally affects plant metabolism, growth, and development, but it also affects leaf hydraulic conductance by modifying the vascular and extra-vascular compartments (Leclerc, 2003; Fitter & Hay, 2012). Temperature-driven effects in hydraulic conductance can be partly explained by viscosity changes of xylem sap and partly by cell membrane permeability (Cochard et al., 2000b; Sack et al., 2004; Sellin & Kopper, 2007; Holbrook & Zwieniecki, 2011). Thus, water viscosity is an essential characteristic to take into account in hydraulic measurements. In addition to temperature, fluid viscosity depends on solute content, but xylem sap solute concentrations are so small that they do not influence viscosity measurably (Cruziat et al., 2002). With increasing temperature, water viscosity decreases and cell membrane permeability rises, both resulting in higher hydraulic conductance (Cochard et al., 2000b; Matzner & Comstock, 2001; Sack et al., 2004; Sellin & Kopper, 2007). Sellin and Kopper (2007) demonstrated that about a third of the temperature effect on K_L of little-leaf linden (*Tilia cordata* Mill.) in field conditions was attributable to shifts in the viscosity of water and two-thirds to shifts in protoplast permeability (i.e., symplastic conductance).

The hydraulic system of plants operates under considerable tension, i.e. below normal atmospheric pressure. This means that trees live under the constant threat of rupture of the water columns and xylem cavitation (Cochard, 2006; Brodersen et al., 2019). Continuous water columns in the xylem conduits may break, xylem vessels and tracheids may embolize, and water supply to transpiring leaves may be disrupted (Sperry & Sullivan, 1992; Cochard, 2006; Brodersen et al., 2019; Jacobsen et al., 2019). There is always some degree of native embolism throughout the year, even in well-watered trees (Tyree & Ewers, 1991; Cruziat et al., 2002). It is surprising that even trees growing in temperate ecosystems have relatively high levels of embolism (37–94%; Klein et al., 2018). Many studies report a trade-off between cavitation safety and transport efficiency in trees (Cochard et al., 2004; Hacke et al., 2006; Meinzer et al., 2008; van der Sande et al., 2019; Yao et al., 2021), but this does not apply to lianas (van der Sande et al., 2019). Cavitation-induced embolism decreases xylem hydraulic conductance, brings about stomatal closure, and begins to limit transpiration and photosynthesis (Meinzer et al., 2001; Trifilò et al., 2011; Choat et al., 2012; van der Sande et al., 2019). Cavitation vulnerability is associated with wood anatomy (de Oliveira et al., 2018; Mrad et al., 2018), with vessel diameter being among the relevant traits (Hacke et al., 2017). Generally, species with long and wide vessels, like ring-porous trees, are efficient water transporters, but they are also vulnerable to cavitation. Other species with smaller conduits are much more secure against hydraulic failure (Hacke et al., 2006). Also within a species, larger vessels tend to be more vulnerable to cavitation than narrow ones (Jacobsen et al., 2019).

Substantial differences exist in vulnerability to cavitation among different plant species (Sperry & Sullivan, 1992; Sperry et al., 1994; Cruziat et al., 2002; Meinzer et al., 2008) and between different organs in the same individual (Cruziat et al., 2002; Choat et al., 2005). This pattern is consistent with the hydraulic

vulnerability segmentation hypothesis, which states that distal parts of the plant should be more vulnerable to embolism than trunks (Choat et al., 2005; Johnson et al., 2016). Consequently, during drought, embolism occurs first in distal branches and leaves, while larger proximal branches and stems will be protected (Meinzer et al., 2001). A similar pattern has also been reported during wintertime in *Picea abies* (L.) H. Karst. growing at the alpine timberline (Charrier et al., 2017). Losses of conductivity are characterized with vulnerability curves describing the relationship between loss of hydraulic conductivity (the percent loss of conductivity, PLC) and xylem pressure or water potential (Choat et al., 2012; Klein et al., 2018; Brodersen et al., 2019; Konrad et al., 2019). The most commonly used index for embolism resistance is Ψ_{50} , describing the point where 50% loss of conductivity occurs (Meinzer et al., 2009; Choat et al., 2012; Brodersen et al., 2019).

Plant hydraulic systems are able to adapt to changes in external conditions (Landsberg et al., 2017). Trees use different strategies to cope with cavitation: closing stomata (Hacke et al., 2006; Nardini et al., 2011b; Trifilò et al., 2011); producing new functional xylem from cambium (Hacke & Sperry, 2001; Nardini et al., 2011a, 2011b), which is characteristic of ring-porous species, especially oaks (Sperry et al., 1994); use of stored water; positive root pressure; and refilling embolized xylem conduits (Hacke & Sperry, 2001; Nardini et al., 2011a, 2011b; Secchi & Zwieniecki, 2012; Landsberg et al., 2017; Tomasella et al., 2020). Xylem refilling is related to various structures, like roots, phloem, parenchyma, aquaporins, and xylary chloroplasts (Klein et al., 2018). Living parenchyma cells associated with xylem, called vascular associated cells (VACs), are directly involved in the refilling process (Pagliarani et al., 2019; Secchi et al., 2021). Embolism refilling under tension is a process demanding energy. Therefore it needs a suitable supply of carbohydrates to change the pre-existing free-energy gradients (Secchi & Zwieniecki, 2012). A significant correlation occurs between stem hydraulics and non-structural carbohydrate contents (NSC) in drought and frost stress conditions (Trifilò et al., 2017; Tomasella et al., 2020). During drought, sugars are accumulated in xylem parenchyma, apoplast, and VACs (Tomasella et al., 2020; Secchi et al., 2021). Hydraulic recovery requires the biological activity of VACs via chemical priming (Secchi et al., 2021), which involves a drop in apoplast pH and the accumulation of sugars (Secchi & Zwieniecki, 2012; Pagliarani et al., 2019). Therefore NSC concentration decreases, starch content increases, and xylem apoplast pH declines (Salleo et al., 2004; Secchi & Zwieniecki, 2016; Trifilò et al., 2017; Pagliarani et al., 2019; Tomasella et al., 2020). A complex network of coordinated molecular and biochemical signals is activated by hydraulic recovery at the interface between xylem and parenchyma cells (Pagliarani et al., 2019).

1.4. Physico-chemical properties of xylem sap and ionic effect

Long-distance water transport in plants is commonly treated as a passive process affected by physical and geometrical features of the xylem conduits, although it is admitted that the mechanisms based on the cohesion-tension theory may be too simplistic (Meinzer et al., 2001; Holbrook & Zwieniecki, 2011). Nowadays, there is much evidence that plants are capable of regulating xylem hydraulic conductivity in a short time scale by adjusting xylem sap ionic content (Zwieniecki et al., 2001, 2003; Gascó et al., 2006, 2008; Nardini et al., 2007, 2011b; Aasamaa & Söber, 2010; Cochard et al., 2010; Jansen et al., 2011). This phenomenon was shown first by Martin H. Zimmermann in 1978 (Zimmermann, 1978). This issue has aroused broader interest among researchers in the 21st century. Several studies have shown that xylem hydraulic conductivity of stems or branches increases by perfusing them with weak salt solutions compared to deionised water (van Ieperen et al., 2000; Zwieniecki et al., 2001, 2003; Gascó et al., 2006, 2008; Aasamaa & Söber, 2010; Cochard et al., 2010; Jansen et al., 2011). Other solutions, like isoosmotic carbohydrate solutions, do not affect xylem hydraulic conductivity. This indicates that this phenomenon cannot be explained purely by the osmotic effects of the perfusate. Xylem hydraulic conductivity depends on the ionic concentration of xylem sap (van Ieperen et al., 2000), and therefore the phenomenon is called an ionic effect (Nardini et al., 2011b). In many species, xylem hydraulic conductivity increases in response to changes in xylem sap ionic concentration, but it is not a universal phenomenon for all species (Trifilò et al., 2008; Holbrook & Zwieniecki, 2011; Nardini et al., 2011b).

In most studies, KCl is used in hydraulic experiments to evaluate the ionic effect (Zwieniecki et al., 2001, 2003; Gascó et al., 2006, 2008; Aasamaa & Söber, 2010; Cochard et al., 2010; Jansen et al., 2011). K^+ is the most important cation in plant biomass (Cornut et al., 2021) and it accounts for about 50% of the total ion content of the xylem sap (Herdel et al., 2001; Siebrecht et al., 2003). Potassium is among the essential elements needed in various physiological processes of plants (Liesche, 2016; Shabala, 2017; Davis et al., 2018; Mirande-Ney et al., 2020). Some studies have also applied NaCl solution, which has a weaker effect than KCl (Gascó et al., 2006, 2008) and Ca^{2+} , which reduces the magnitude of the ionic effect (van Ieperen & van Gelder, 2006; van Ieperen, 2007), although this is not a universal response (Nardini et al., 2007). Commonly, deionised water has been used as a reference solution (Zwieniecki et al., 2001, 2003; Gascó et al., 2006, 2008; Aasamaa & Söber, 2010; Cochard et al., 2010), although it has certain disadvantages. Deionised water may change the plant's inherent xylem hydraulic conductivity because it is not comparable with the properties of the xylem sap *in vivo* (van Ieperen & van Gelder, 2006; van Ieperen, 2007), which always contains various ions in low concentrations (Herdel et al., 2001). The use of deionised water as a reference solution may overestimate the ionic effect because we underestimate the natural fluidity of xylem sap (van Ieperen, 2007).

Several hypotheses have been proposed on how the ionic effect works. One hypothesis states that metal cations occurring in the xylem sap influence the pectic matrix of the pit membranes. In the presence of cations, the pectic matrix in pit membranes will shrink. As a consequence, nanometer-sized pores in the pit membrane expand, and xylem hydraulic conductivity increases. At low ionic concentrations in the xylem sap, the pectic matrix will swell, which leads to narrower pores and a decrease in xylem hydraulic conductivity (Zwieniecki et al., 2001; Holbrook & Zwieniecki, 2011; Nardini et al., 2011b). This hypothesis is supported by Boyce et al. (2004), who found a correlation between lignification patterns of water-conducting cells and ion-mediated flow rate in the xylem. The distribution of hydrophilic polysaccharides and hydrophobic lignin probably affect the hydraulic properties of the xylem (Boyce et al., 2004).

The sample length (Gascó et al., 2006), degree of vessel grouping and inter-vessel traits may also influence the ionic effect (Jansen et al., 2011). It has also been proposed that the pit membranes behave like a gelled non-porous structure (Cochard et al., 2010). The studies with a liquid-phase atomic force microscope support that idea: a layer of hydrogel is located on the surface of the membrane (Lee et al., 2012). Lee et al. (2012) show that the ionic effect involves changes in permeability and thickness of the pit membrane hydrogel. Fully hydrated pit membranes under a scanning electron microscope look like a continuous surface of soft material covering fibres. Perfusion with 50 mM KCl solution decreased overall membrane microfibril pectin hydrogel thickness and increased surface roughness significantly (Lee et al., 2012). Some studies show that pectin may not be present in the pit membranes of all species (Choat et al., 2008; Doorn et al., 2011). For example, instead of pectin-hydrogel pit membranes, gymnosperms and lycopods have highly porous margins and do not respond to the presence of K^+ (Holbrook & Zwieniecki, 2011). Therefore, the swelling and shrinking hypothesis is not universal for all woody plants. Some authors suggest that electroviscosity of the bordered pit membranes is responsible, at least partially, for this phenomenon (Doorn et al., 2011; Nardini et al., 2011b; Santiago et al., 2013). There is still much unknown concerning this mechanism in different species that requires further research.

Flushing branches with boiling water or freezing them with liquid nitrogen does not affect the ion-mediated increase in water flow (Zwieniecki et al., 2001; Gascó et al., 2006). That means living cells do not directly affect changes in xylem hydraulic resistivity (Zwieniecki et al., 2001). Xylem hydraulic efficiency depends on phloem properties, due to ion circulation between the xylem and phloem (Cernusak & Marshall, 2001; Zwieniecki et al., 2004; Domec & Pruyn, 2008; López et al., 2015; Konrad et al., 2019). Phloem girdling, removing surface tissues around the woody branch or stem (Rademacher et al., 2019), blocks phloem transport from the branch and leads to starch and sugar accumulation in leaves above the girdle. Simultaneously, one can see the induction of stomatal closure and a decrease in photosynthesis through a feedback loop (Cernusak & Marshall, 2001; Murakami et al., 2008).

Potassium availability and drought stress, combined, have a substantial effect on the functioning of plants (Oddo et al., 2020). In drought conditions, potassium ions in the xylem sap have a primary role in the ion-mediated enhancement of hydraulic conductance (Trifilò et al., 2011, 2014; Oddo et al., 2020). The liquid in nonfunctional vessels contains an increased level of sugars and ions compared to functional vessels in order to create an osmotic gradient (Secchi & Zwieniecki, 2012). Short-term potassium fertilization increases xylem sap $[K^+]$ in well-watered *Laurus nobilis* L. plants, leading to enhanced hydraulic efficiency (Oddo et al., 2011). At the same time, when potassium is added to previously drought-stressed plants, there is no short-term increase in $[K^+]$ in the xylem sap, nor in hydraulic efficiency (Oddo et al., 2014).

In addition to ionic contents, variations in pH of the xylem sap may play a role in regulating plant hydraulic conductance. Zwieniecki et al. (2001) showed that the natural pH range (5.8 to 8.0) of xylem sap does not significantly affect plant hydraulics, but low pH increases flow rates remarkably. Change in xylem sap pH in drought conditions, when the transpirational flux is reduced, is well documented (Bahrun et al., 2002; Sobeih et al., 2004; Secchi & Zwieniecki, 2016). So, embolized vessels exhibit lower apoplast pH than hydrated ones (~5.4 and ~6.2 respectively; Secchi & Zwieniecki, 2012), but this response is not universal (Sharp & Davies, 2009). Xylem sap pH is an important characteristic influencing sugar transport across cellular membranes (Secchi & Zwieniecki, 2012, 2016). Lower xylem apoplast pH in water-stressed plants leads to sugar accumulation in the xylem apoplast (Secchi & Zwieniecki, 2016). Xylem sap osmolality is also a relevant characteristic having an effect on water transport efficiency, pressure gradients, and the turgor pressure of living cells in plants (López-Portillo et al., 2014).

1.5. Aims of the thesis

This doctoral thesis aims to give new insights into the role of the physico-chemical properties of xylem sap in regulating trees' hydraulic conductance. Most of the studies on the ionic effect have been conducted in laboratory conditions (van Ieperen et al., 2000; Zwieniecki et al., 2001, 2003; Gascó et al., 2006; van Ieperen & van Gelder, 2006) and in the Mediterranean climate (Gascó et al., 2006, 2007; Trifilò et al., 2008, 2011; Nardini et al., 2010, 2012). Only a few studies on this topic have been performed in northern temperate trees (Aasamaa & Söber, 2010; Sellin et al., 2013). In this thesis, we focus on exploration of trees growing in the field. We analyse how environmental conditions, especially light availability and quality, affect the xylem sap and hydraulic properties in temperate broadleaved trees growing in field conditions. This thesis provides novel information on the ionic effect and trees' hydraulic properties in northern forests.

This study analyses the relationship between xylem sap properties and the hydraulic conductance of stems in hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) and silver birch (*Betula pendula* Roth), both economically

important hardwoods in northern Europe. We aimed to explore different aspects of these relationships. First, we looked at circadian patterns because there is scanty information about the daily dynamics of the hydraulic efficiency of trees. Most previous studies are incomplete because they are missing nightly measurements (Bucci et al., 2003; Brodribb & Holbrook, 2004; Lo Gullo et al., 2005; Cordeiro et al., 2009; Johnson et al., 2009; Voicu & Zwiazek, 2011; Öunapuu & Sellin, 2013; Locke & Ort, 2015). From environmental characteristics we focused on irradiance and air temperature, the most influential factors driving circadian patterns in plant hydraulic properties. Second, we wondered whether phloem girdling, a blocking of phloem transport, affects hydraulic and xylem sap properties. Third, we tested whether short-term changes in light conditions impact stem hydraulic efficiency, i.e., a light-mediated modulation of stem hydraulic conductance. We also studied the effect of different light wavelengths on leaf and shoot hydraulic efficiency and the distribution of the resistance in shoots.

The objectives of the doctoral thesis are as follows:

- To simultaneously ascertain circadian patterns of hydraulic conductivity and the physico-chemical properties of xylem sap *in situ* (**Paper I**).
- To evaluate the impact of phloem girdling on branch hydraulic conductance and the physico-chemical properties of the xylem sap (**Paper II**).
- To evaluate the impact of light quality on leaf and shoot hydraulic properties (**Paper III**).
- To test light-mediated modulation of stem hydraulic conductance (**Paper IV**).

2. MATERIALS AND METHODS

2.1. Characterization of the experimental area and sample trees

First study site was the Free Air Humidity Manipulation (FAHM) facility, located at Rõka village (58°14'N, 27°17'E; 40–48 m ASL), eastern Estonia, where air humidity is artificially increased in field conditions. The FAHM system enables air relative humidity (RH) to be elevated up to 18% compared to the ambient level, and the mean increase in RH across the growing season is up to 7%. The aim of the experimental site is to investigate the effect of increased RH on the growth and performance of trees in response to the rising atmospheric humidity predicted for northern Europe. The facility was established in 2006–2007 on an abandoned agricultural field. It is a fenced area of 2.7 ha involving nine experimental plots (Ø 14 m) planted with silver birch (*Betula pendula* Roth) and hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) with a stand density 10 000 trees ha⁻¹, surrounded by a buffer zone of hybrid aspens with a stand density 2500 trees ha⁻¹ (Kupper et al., 2011). The study area belongs to the boreo-nemoral vegetation zone in a northern temperate climate. The long-term average annual precipitation in the region is 650 mm, and the average temperature is 17.0 °C in July and –6.7 °C in January. The growing season usually lasts 175–180 days from mid-April to October. The soil is a fertile endogenic mollic planosol (WRB) with an A horizon thickness of 27 cm. Total nitrogen content is 0.11–0.14%, C/N ratio is 11.4, and pH is 5.7–6.3.

Silver birch (**Paper IV**) saplings growing in the experimental plots and hybrid aspens (**Papers I and II**) growing in the buffer zone served as sample trees. For **Paper I**, the studies were carried out in July and August 2012. We collected 2×112 branches (i.e., two neighbouring branches per tree simultaneously) from 7-year-old aspen trees. The branches for every measurement event were cut from different trees, 112 trees altogether. The sample trees' mean height (±S.E.) was 5.12 ± 0.08 m; the branches were cut from the middle third of the crowns (relative height 0.25–0.60). Studies for **Paper II** were performed in August 2010. We sampled ten 5-year-old aspen trees with a mean height of 4.0 ± 0.09 m. From each tree two neighbouring branches (mean height above the ground 129 ± 3.6 cm and mean length 147 ± 4.4 cm) of equal size were examined. Material for **Paper IV** was collected from July to August 2009. The sample branches of silver birch were cut from three heights in the canopy: on average at 53 cm (mean length 91 cm), 177 cm (mean length 112 cm), and 227 cm (mean length 91 cm) above the ground. Altogether, 36 branches (2 treatments × 3 sample plots × 2 trees × 3 canopy positions/heights) were sampled for hydraulics.

The second study site was situated in Järvselja Experimental Forest (58°16'N, 27°16'E, elevation 38–40 m ASL), eastern Estonia, where the stand is composed of *B. pendula* Roth 46%, *Picea abies* (L.) Karst. 44%, *Pinus sylvestris* L. 8%, and

Populus tremula L. 2% of the total basal area. The data on precipitation, temperature and growing season are given hereinabove. The annual global short-wave radiation sum in the region averages $3,518 \text{ MJ m}^{-2}$, and the annual radiation budget is $2,552 \text{ MJ m}^{-2}$ (Sellin & Kupper, 2005a, 2005b). The area has a gleyed pseudopodsol soil formed on a loamy till and characterized by a large water storage capacity (Niinemets & Kull, 2001). For **Papers III** and **IV**, 15–40 cm long shoots were sampled from the lower (shade-exposed shoots) and upper thirds (sun-exposed shoots) of 25- to 30-year-old silver birches. Mean tree height was 15.5–19.4 m and diameter at breast height was 10.3–16.2 cm. For **Paper III**, altogether 108 shoots were sampled: 3 trees \times 2 canopy positions \times 3 light colours \times 3 exposure times \times 2 replications.

2.2. Environmental characteristics at the FAHM site

At the FAHM site, various environmental variables are recorded continuously. In our study, we used photosynthetic photon flux density (PPFD) measured using LI-190 quantum sensors (Li-Cor Biosciences, Lincoln, NE, USA), air temperature (T_A), and relative humidity (RH) measured with HMP45A humidity/temperature probes (Vaisala, Helsinki, Finland), bulk soil water potential (Ψ_s) measured with EQ2 equitensiometers (Delta-T Devices, Burwell, UK) at depths of 15 and 30 cm. The environmental sensors' readings were stored as average values every 10 min with a DL2e data logger (Delta-T Devices). Atmospheric vapour pressure deficit (VPD) was calculated as the difference between the saturation vapour pressure (i.e., the maximum amount of water vapour that can be held in the air) and the actual vapour pressure (Bonan, 2015). Light availability within the canopy of the experimental plots was estimated using the hemispherical photographic technique (Hale & Edwards, 2002). In **Paper IV**, photographs ($n = 108$) were taken at different heights in the canopy with a Coolpix digital camera (Nikon Corp., Tokyo, Japan) equipped with a fisheye lens, and the hemispherical images were analysed by applying WinSCANOPY, Vers. 2.1A software (Regent Instruments, Ottawa, Canada).

2.3. Laboratory experiment on light impact

In the evening, shoots of *B. pendula* were cut under water and put into beakers, the basal ends submerged in water (**Papers III** and **IV**). In the laboratory, the shoots were put into plastic flasks filled with deionized, filtered (Direct-Q3 UV water purification system; Millipore SAS, Molsheim, France), and freshly degassed water (T-04-125 ultrasonic-vacuum degasser; Terriss Consolidated Industries, Asbury Park, NJ, USA), and rehydrated overnight in a dark room. For **Paper III**, in the morning the shoots were exposed to light of photosynthetic photon flux density (PPFD) of $200\text{--}250 \text{ mmol m}^{-2} \text{ s}^{-1}$ for 1, 3 or 5 h before the hydraulics measurements. The PPFD was measured with a LI-190 quantum

sensor and the energy flux within the band of photosynthetically active radiation with a SKE 510 energy sensor (Skye Instruments, Llandrindod Wells, UK). Shoots were exposed before and during the hydraulic measurements to light from different sources: blue light from metal halide lamps (Artcolour MH-T Blue, 400 W; Philips, Eindhoven, the Netherlands) with a spectral emission maximum at 450–460 nm; white light from high pressure sodium lamps (Master SON-T PIA Agro, 400 W; Philips) with a wide spectral emission band of 550–710 nm and with additional peaks in the blue band; red light from the Master SON-T PIA Agro lamps used in combination with 026 Bright Red colour filters (Lee Filters, Andover, UK), which lacked wavelengths below 600 nm.

In **Paper IV**, in the morning the shoots were exposed to light (Master SON-T PIA Agro lamps) for 7 h before the conductance measurements. Both shade (95 shoots in all) and sun (96 shoots in all) shoots were exposed to four different irradiance levels: PPFD was 70, 140, 330 and 610 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In both studies, irradiance was controlled and modified by changing the distance from the lamps. Air above the shoots was agitated with a fan to avoid local temperature gradients.

2.4. Phloem girdling

Two neighbouring branches of equal size from aspen trees were sampled for gasometric and hydraulic characteristics (**Paper II**). The phloem was girdled at the branch base on one branch, while the second branch was left untreated as a control. Two 1-cm strips of bark (cortex and phloem) were removed with a razor blade without damaging the xylem: one at the branch basal end, the second ~15 cm above the first. The girdled regions were instantly covered with silicon grease and wrapped tightly in adhesive plastic tape to prevent desiccation. Physiological measurements were made immediately before phloem girdling and 1, 2, and 3 days after the manipulation. The girdled and control branches were sampled simultaneously in the midday period (10–14 h). Net photosynthetic rate (P_N) and stomatal conductance to water vapour (g_s) were measured with a LCpro+ portable photosynthesis system (ADC BioScientific, Great Amwell, UK) at saturating photosynthetic photon flux density of 1196 $\mu\text{mol m}^{-2} \text{s}^{-1}$, ambient CO_2 concentration of 360 $\mu\text{mol mol}^{-1}$, water vapour pressure of 1.5 kPa and temperature of 25 °C.

2.5. Measurement of plant hydraulic properties by water perfusion method

The cut ends of the sample branches were recut under water and immediately measured hydraulically at PPFD of 120–150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Master SON-T PIA Agro lamps; **Paper IV**) or in natural environmental conditions *in situ* (**Paper I**). In the last case, we used a shelter with a transparent polycarbonate roof lacking

walls to protect equipment against direct rainfall. Hydraulic conductance of the whole branch (K_{wb}) and their parts – leaf blades (K_{lb}), petioles (K_p), bare branch (K_B) – were determined by the water perfusion method using a high-pressure flow meter (HPFM; Dynamax, Houston, TX, USA), and by removing leaf blades and petioles in sequence. The HPFM method was applied also in the experiment to test light spectral effects (**Paper III**). The HPFM was applied in a quasi-steady-state mode, applying the pressure until leaves were infiltrated. That procedure removes emboli from the vascular system and fills the empty vessels (Nardini et al., 2005). Thus, these readings show plant hydraulic efficiency in a water-saturated state. In **Paper I**, hydraulic measurements were performed every 3 hours to estimate circadian patterns.

The hydraulic conductance of leaf blades (K_{lb}) was calculated as follows:

$$K_{lb} = (K_{wb}^{-1} - K_{B+p}^{-1})^{-1} \quad (1)$$

where K_{B+p} is the hydraulic conductance of a branch together with petioles. The hydraulic conductance of petioles (K_p) was calculated as:

$$K_p = (K_{B+p}^{-1} - K_{lb}^{-1})^{-1} \quad (2)$$

Leaf and branch temperatures were recorded using MT2 fast-response temperature probes (Delta-T Devices) during the hydraulic measurements. In **Paper IV**, after achieving stable readings with HPFM for the leafless branch, the distal branch part was cut off. The remaining 15- to 20-cm basal segment of the branch, left connected to the pressure coupling, was perfused again to determine the specific hydraulic conductivity of branch-wood (k_{bw}), to be calculated as follows:

$$k_{bw} = \frac{K_{seg} \cdot l}{A_x} \quad (3)$$

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

After completing the hydraulic measurements, all leaves were collected, and the total leaf blade area was determined with a LI-3100C optical area meter (Li-Cor Biosciences; **Papers I** and **IV**) or with an AM300 digital area meter (ADC BioScientific, Great Amwell, UK; **Paper III**). The hydraulic characteristics were corrected for dynamic viscosity of water at given temperature.

2.6. Evaluating hydraulic conductance by evaporative flux method

In **Papers II** and **IV** we estimated hydraulic conductance of shoot (K_S) and leaves (K_L) by the evaporative flux method (Wullschleger et al., 1998; Brodribb & Holbrook, 2003; Sellin et al., 2008) under steady-state conditions and calculated it according to the Ohm's law analogy:

$$K = \frac{E}{\Delta\Psi} \quad (4)$$

where E is the transpiration rate expressed per unit leaf area, and $\Delta\Psi$ is the water potential drop across a particular segment. E was measured at the leaf surface with an LI-1600M steady-state diffusion porometer (Li-Cor Biosciences), sampling three to four leaves per shoot. Leaf temperature (T_L) was measured with fine copper – constantan thermocouples installed in the porometer. Immediately after the porometric measurements, the bulk leaf water potential (Ψ_L) in three leaves per shoot was determined by the balancing pressure technique using a Scholander-type pressure chamber. The leaves for porometric and pressure chamber measurements were chosen randomly, from different parts of the shoot.

Branch water potential (Ψ_B) was estimated by applying the method of bagged leaves (Nardini et al., 2001; Brodribb & Holbrook, 2003) using two leaves per shoot prepared in previous evening. These leaves were enclosed in small minigrip bags, sealed with tape and wrapped in aluminum foil, and then placed overnight with shoots in a dark room. Water potential of the nontranspiring (bagged) leaves, which was presumed to have equilibrated with the xylem water potential of the branch, was taken as a proxy of Ψ_B . After the pressure chamber measurements, total area of leaf blades was determined with an AM300 area meter. The hydraulic conductance of leafless branch (K_B) was calculated as follows:

$$K_B = (K_S^{-1} - K_L^{-1})^{-1} \quad (5)$$

The values of hydraulic conductance were scaled by leaf area and standardized for the dynamic viscosity of water at a given temperature.

2.7. Extraction of xylem sap and determination of its physico-chemical properties

To measure the physico-chemical properties of xylem sap, we cut the sample branch from a tree, beforehand removing all leaves from the branch to stop transpiration. The sap was extracted from branch segments at a pressure of 2.0 MPa generated by a pressure chamber (Model 1000; PMS Instrument Company, Albany, OR, USA) according to Stark et al. (1985). Details of the procedure have

been described in Sellin et al. (2011). The sap samples collected in 1.5-ml Eppendorf tubes were immediately measured for potassium ion concentration ($[K^+]$) using a C-131 potassium ion meter (Horiba, Kyoto, Japan). Sap electrical conductivity (σ_{sap}) and pH were determined using an electric conductometer (Twin Cond B-173; Horiba) and pH meter (Twin B-212; Horiba), respectively. We also determined the osmolality (Osm) of the xylem sap using a Vapro 5600 vapor pressure osmometer (Wescor, Logan, UT, USA).

In **Papers I, III and IV**, $[K^+]$ was measured simultaneously in pairs of branches taken from the same tree and height – one was a branch used for hydraulic measurements, and the other was its closest unperfused neighbour. In **Paper II**, xylem sap physico-chemical properties were measured in two neighbouring branches (phloem girdling treatment and control) on the third day after girdling, subsequent to the final gasometric and water potential measurements.

2.8. Laboratory experiment to assess the effect of $[K^+]$ on xylem hydraulic conductivity

An experiment was conducted from July to August 2018. The experiment was carried out on branches of 5-year-old hybrid aspens collected from the FAHM experimental plots. The mean tree height (\pm SE) was 5.57 ± 0.17 m. Branches with a mean length of 1.75 ± 0.06 m were collected on average from a height of 2.12 ± 0.12 m at 9 a.m. After cutting, the branches were immediately taken to the field laboratory located at the FAHM site. A specimen with a length of 14.0 ± 0.1 cm (mean diameter measured under bark 10.5 ± 0.1 mm) was cut from the basal part of the branch without leaves and placed into a cavitation chamber attached to a Model 600-EXP pressure chamber (PMS Instrument Company). Cavitation of the stem segments was induced using an air-injection technique applying a pressure of 2.0 MPa for one hour. After that, the specimens were sampled hydraulically to determine the initial hydraulic conductance of the embolised stem segment (K_{in}). The hydraulic measurements were conducted using a XYL'EM xylem embolism meter (Bronkhorst, Montigny-Les-Corbeilles, France) based on a high-resolution liquid mass flowmeter (Cochard et al., 2000a). The initial and subsequent stem hydraulic conductances were measured under low pressure (<5 kPa). Then the specimens were saturated with water by applying flushes (10 flushes, duration 1.5 min) under 0.2 MPa with solutions differing in $[K^+]$. Based on native $[K^+]$, we used three different K^+ solutions in our experiment – 0% (deionized water), 50% (65 ppm), and 100% (130 ppm) of the native concentration. Native $[K^+]$ around midday was determined at the beginning of the study period. Hydraulic conductance was recorded continuously, and, after the last flushing, maximum stem hydraulic conductance (K_{max}) was recorded. Respective values of specific hydraulic conductivity of xylem (k and k_{max}) were calculated based on the measurements and specimen dimensions according to equation (3).

The percentage loss of stem hydraulic conductance (PLC) was calculated as:

$$\text{PLC} = \frac{100 \cdot (k_{\max} - k)}{k_{\max}} . \quad (6)$$

The effect of water saturation level on xylem specific conductivity (k) was analysed by using the following asymptotic function:

$$k = \frac{k'_{\text{sat}} \cdot c_1 \cdot (\text{Fl} + q)}{k'_{\text{sat}} + c_1 \cdot (\text{Fl} + q)} \quad (7)$$

where k'_{sat} is the estimate of maximum conductivity at an infinitely saturated state, Fl is the number of flushes, and c_1 is the initial slope of the response curve.

$$q = \frac{c_2}{c_1}, \quad (8)$$

if it is assumed that the initial slope of the curve is nearly linear. c_2 is the value of k before flushing (i.e., an estimate of initial conductivity), and is given by the intercept on the ordinate.

2.9. Data analysis

Statistical data analysis was carried out using Statistica, Version 7.1 (StatSoft Inc., Tulsa, OK). One-way and two-way analyses of variance (ANOVA) and co-variance analysis (ANCOVA) were performed using the General Linear Models module. Type III or Type IV sums of squares were used in the calculation, depending on the particular data set. The normality of data and homogeneity of variances were checked using the Kolmogorov–Smirnov D-statistic and the Levene test, respectively. When necessary, logarithmic or complex transformations were applied to the data to meet the assumptions for ANOVA. During the analysis, insignificant covariates were removed from the analysis models step by step. *Post hoc* mean comparisons were conducted using the Tukey's HSD test. Pearson's correlations and linear or nonlinear regressions fitted by the least-squares method were used to assess relationships between the studied characteristics and independent variables.

3. RESULTS AND DISCUSSION

3.1. Variation in physico-chemical properties of xylem sap

$[K^+]$ of xylem sap varies significantly within the tree canopy, between different years and also on the diurnal scale (Table 1). $[K^+]$ increased in HPFM-perfused and unperfused branches of silver birch from the bottom to the top of the crown at the FAHM site (Figure 4 in **Paper IV**). We saw a similar trend in large trees growing in a natural forest stand, where $[K^+]$ averaged 16.6 ± 1.6 ppm for shade shoots and 24.3 ± 3.0 ppm for sun shoots (**Paper III**). A similar spatial pattern was also found in another study in silver birch (Sellin et al., 2013), where native xylem sap potassium ion concentration increased from 81 ± 6.7 ppm at the crown base to 111 ± 8.6 ppm in the upper crown ($P < 0.001$). Similar spatial trends in $[K^+]$ and sap electrical conductivity (σ_{sap}) have been recorded also in laurel plants (*Laurus nobilis* L.; Nardini et al., 2010). In hybrid aspen (**Paper I**), $[K^+]$ varied with tree height (H_T), and σ_{sap} varied with H_T and relative branch height (H_{Brel}). $[K^+]$ and σ_{sap} increased with H_{Brel} and decreased with increasing H_T , confirming the same trend – xylem sap ionic content increases from the bottom to the top. Branches sampled from taller trees were located lower on a relative scale. Shoots located relatively higher in the canopy exhibited higher $[K^+]$ in the xylem sap. Our data support the idea that the ionic content of xylem sap is upregulated with increasing irradiance (Schurr, 1998; Nardini et al., 2010). Upper-canopy branches are more exposed to sun and wind, both enhancing transpiration and leading to greater water losses from leaves. An effective water transport system is required in order to compensate for increasing water losses, keep stomata open, and avoid tissue dehydration. Furthermore, ions in the xylem sap contribute to the process limiting embolism development and keeping the hydraulic system working.

Table 1. Mean native potassium ion concentrations of xylem sap in silver birch and hybrid aspen in different case studies.

Species	Year	Tree location	Paper	Native $[K^+]$ (ppm)	Clarification
Silver birch	2009	average of H and C plots in FAHM site	IV	43–170	$[K^+]$ in different tree heights
	2009	Järvelja forest	III	7–73	$[K^+]$ in different tree heights
	2012	Järvelja forest	unpublished data	9–100	$[K^+]$ in different tree heights
Hybrid aspen	2010	buffer zone in FAHM site	II	8–41	$[K^+]$ in control branches
	2011	average of H and C plots in FAHM site	unpublished data	57–230	$[K^+]$ in different tree heights
	2012	buffer zone in FAHM site	I	54–230	$[K^+]$ circadian range
	2018	average of H and C plots in FAHM site	unpublished data	130 (average)	$[K^+]$ on midday

Water perfusion under high pressure (**Paper IV**) diluted the xylem sap and caused $[K^+]$ to decline roughly by half ($P < 0.001$) in silver birch. Interestingly, the acropetal increasing trend within the canopy remained after flushing the branches for 20 minutes with deionized water, which should fill the xylem conduits with deionized water. This suggests that living tissues were probably enriching the xylem sap with potassium ions during perfusion with HPFM. Metzner et al. (2010) showed that adjacent living tissues regulate vessel content by a lateral exchange and potassium ions easily move laterally. We did not find statistically significant differences in $[K^+]$ between control plots and those with increased air humidity (**Paper IV**). In another study in silver birch (Sellin et al., 2013), also no differences in $[K^+]$ were established between the control and elevated humidity conditions. It is meaningful that both studies were carried out on rainy summers. Therefore the efficiency of air humidification treatment remained low, which could be the reason why $[K^+]$ was comparable among the treatments. Environmental conditions at the FAHM site vary remarkably between different growing seasons (Godbold et al., 2014). We saw a high variability in native $[K^+]$ of xylem sap in hybrid aspen and silver birch between different years and different sites (Table 1), although measurements have been made with the same equipment and carried out by the same person. Consequently, single case studies on ionic concentrations of the xylem sap conducted in a particular year or study site cannot sufficiently describe the $[K^+]$ dynamics of particular species.

$[K^+]$ and σ_{sap} demonstrated pronounced daily courses in hybrid aspen (Figure 1; **Paper I**). $[K^+]$ and σ_{sap} increased rapidly in the morning after sunrise and reached their maxima at noon or after that (12–15 h), then they decreased gradually and stayed pretty stable during the night. Similar daily patterns have been described for hybrid poplars (Siebrecht et al., 2003) and Mediterranean trees (Trifilò et al., 2011, 2014), but it is not a universal pattern for all vascular plants. Herdel et al. (2001) demonstrated an increase in $[K^+]$ of xylem sap in *Ricinus communis* L. plants in the evening or during the dark period at night. In continuous light, diurnal variations in nutrient concentrations of the xylem sap disappear, showing that they are associated with light availability (Herdel et al., 2001).

The circadian patterns of $[K^+]$ and σ_{sap} in aspens depended significantly on soil water status and atmospheric conditions (**Paper I**). The ionic content of xylem sap was strongly influenced by photosynthetic photon flux density (PPFD), although $[K^+]$ and σ_{sap} were better associated with atmospheric evaporative demand, AED (Table 1 in **Paper I**). Xylem sap osmolality (Osm) was also highest at midday, during the period of highest transpirational water loss, and lowest in the late afternoon (18 h). After that it increased gradually during the night (Figure 1). Osmolality may be highest also in the morning (Andersen et al., 1995; Sobrado & Ewe, 2006) and lowest at midnight (Andersen et al., 1995), as reported for other species. Osm depended only on PPFD in hybrid aspens. This indicates that at sufficient water supply, daily dynamics of low molecular weight compounds (cations, anions, sugars, amino acids, organic acids, etc.) in the xylem sap are also primarily driven by light conditions.

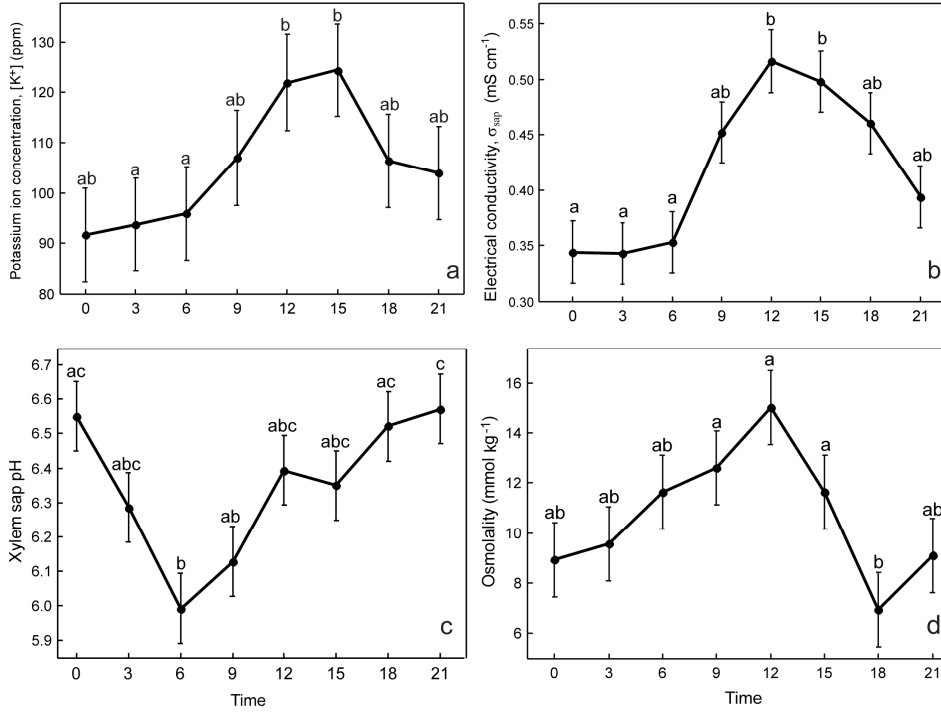


Figure 1. Daily dynamics of potassium ion concentration ($[K^+]$, **a**), electrical conductivity (σ_{sap} , **b**), pH (**c**) and osmolality (Osm, **d**) of xylem sap in hybrid aspen. The vertical bars indicate \pm SE of the means.

The diffusion-supplied nutrients (such as K^+) move to the roots primarily via diffusion; therefore, they are less affected by transpiration-driven mass flow (Tullus et al., 2012). However, potassium uptake depends on water accessibility (Ge et al., 2012). Water is held in soil pore space under tension by capillary forces (Sperry et al., 2002). If the soil dries, then soil hydraulic conductivity and contact between the root surface and soil solution declines (Herdel et al., 2001; Sperry et al., 2002). Only a small fraction of total soil K is available to plants (Sardans & Peñuelas, 2015; Cornut et al., 2021), and soil drying decreases available K^+ uptake (Ashley et al., 2006; Sardans & Peñuelas, 2015). For example, $[K^+]$ in the xylem sap of grapevines was higher in well-watered plants compared to water-stressed ones (Oddo et al., 2020). Under water deficit, xylem sap $[K^+]$ declines in *Zea mays* L. leaves (Bahrun et al., 2002) and in both eucalypt leaves and stems (Santos et al., 2021). At the same time, it has been shown that drought stress raises branch and shoot xylem sap $[K^+]$ in Mediterranean trees (Trifilò et al., 2011, 2014). $[K^+]$ increased with decreasing RH in aspen saplings, illustrating the same trend (Table 1 and Figure 5 in **Paper I**). When VPD is lower, plants lose less water and the soil remains moister. In hybrid aspens, $[K^+]$ also increased with rising soil water potential. Soil water potential measured at a depth of 30 cm (Ψ_{S30}) and relative air humidity (RH) combined described nearly half (49%) of

the total variation in $[K^+]$ (Figure 5 in **Paper I**). Our results suggest that K^+ uptake is facilitated in moist soil for trees growing in northern temperate forests. Reduced VPD increases K absorption and accumulation and also promotes root growth in tomato plants (Zhang et al., 2021). In silver birch, low VPD raises the number of absorptive root tips (Kupper et al., 2017).

In *Arabidopsis*, leaf hydraulic conductance (K_L) is regulated by changes in xylem sap pH (Grunwald et al., 2021b), but on the circadian scale we did not see such a relationship in hybrid aspen. The daily pattern of pH differed qualitatively from that of other xylem sap and hydraulic properties, being highest in the evening. In the dark, we saw a rapid decline of pH followed by a gradual increase in the morning (Figure 1; **Paper I**). Root xylem sap pH in *R. communis* demonstrated a similar circadian pattern: it increased from 6.0 at the end of the dark period to 6.6 at the end of the day (Schurr & Schulze, 1995). In *Populus deltoides* L., xylem sap pH of stems and shoots stays relatively constant during the day (6.94–7.18; Aubrey et al., 2011), while in congeneric hybrid aspen, we recorded substantial diurnal pH variation (average range of 0.6 units). In *Quercus pyrenaica* Willd., xylem sap pH varied from 6.50 and 6.46 in the afternoon and morning to 6.10 measured at night (Salomón et al., 2016).

In hybrid aspen, xylem sap pH increased with declining soil water potential ($R^2 = 0.242$, $P < 0.001$). A strong inverse relationship has been shown to exist between xylem sap pH and gravimetric soil water content. For example, in tomato (*Lycopersicon esculentum* L.) plants, xylem sap pH increased from pH 5.0 to 8.0 with soil drying (Wilkinson et al., 1998). Such a pH increase has also been detected in other species, but this response is not universal (Sharp & Davies, 2009). Sharp and Davies (2009) did not find a significant change in xylem sap pH in response to drought in many species. Recent studies show how drought declines apoplast pH and leads to sugar accumulation in the xylem (Secchi & Zwieniecki, 2016; Pagliarani et al., 2019; Secchi et al., 2021). On a diurnal scale, soil water potential is fairly constant and we propose that the increase in pH during the daytime and the drop during night-time (**Paper I**) are most likely associated with embolism development and recovery (Sellin et al., 2017b) respectively. Restoration of xylem transport capacity needs chemical priming that involves both drop in sap pH and accumulation of sugars in nonfunctional vessels. The drop in pH triggers an ion efflux from living cells that additionally contributes to apoplastic osmotic concentration (Secchi & Zwieniecki, 2012; Secchi et al., 2021). The positive relationship between VPD and the pH of xylem sap in hybrid aspen hints at the coupling of pH and plant water loss.

We established a strong correlation between $[K^+]$ and xylem sap electrical conductivity (σ_{sap}) of hybrid aspen in **Paper I** ($R^2 = 0.748$, $P < 0.001$) and **Paper II** ($R^2 = 0.907$, $P < 0.001$). Xylem sap always contains different ions and the electrical conductivity turns out to be an appropriate characteristic for estimating total ionic strength of the xylem sap, as it characterizes the total ion content (Siebrecht et al., 2003). The strong correlation between $[K^+]$ and σ_{sap} indicates that potassium ions are prevalent ions and $[K^+]$ is suitable for estimating xylem sap ionic strength. Our results also corroborate the importance of potassium ions in

the regulation of plant water relations. Of course, potassium is a crucial element involved in many physiological processes in plants (Cornut et al., 2021).

3.2. Environmental effects on hydraulic traits

Our results suggest that plant hydraulic conductance is enhanced both as a result of long-term acclimation to light availability as well as a short-term response to incident radiation. Branch hydraulic conductance (K_B) of silver birch increased considerably with light availability, in the same way as $[K^+]$, from bottom to top within the tree crowns (Figure 3 in **Paper IV**). In tall forest trees, sun shoots exhibited ~ 1.3 times higher ($P < 0.001$) hydraulic capacity than shade shoots (Figure 3 in **Paper III**). A similar trend has also been observed in shoots, leaves, and stems of laurel plants (Nardini et al., 2010). An acropetal increase in hydraulic efficiency has been revealed also in hybrid aspen (**Paper I**), where bare branch hydraulic conductance (K_B) depended on tree and branch height characteristics. Branch hydraulic conductance increased with relative branch height in the crown (Figure 6 in **Paper I**). The anatomical study on hybrid aspen branch-wood shows a solid dependence of hydraulically relevant vessel traits on canopy position (Jasińska et al., 2015).

Leaf hydraulic conductance increases rapidly when exposed to light because light is among the primary environmental factors influencing plant demand for water, as well as leaf water transport capacity (Holbrook & Zwieniecki, 2011; Fitter & Hay, 2012). Upper branches and leaves have to cope with higher temperatures and are more exposed to irradiance and wind than shaded branches and leaves. Therefore they experience higher water demand and need an efficient water transport system for normal functioning. The light-induced enhancement of liquid-phase conductance reflects trees' response to environmental gradients developing in forest canopies. In saplings of silver birch, higher hydraulic efficiency of upper-crown leaves is associated with larger vascular bundles and higher vein density per unit area (Sellin et al., 2019). Growing for years in different environments along the vertical canopy profile affects the xylem anatomy of both stems and leaves. Shade leaves have a lower need to invest carbon into producing an efficient venation network than sun leaves (Woodruff et al., 2008; Noyer et al., 2017; Alber et al., 2019; Sellin et al., 2019, 2021).

We observed light-mediated effects on K_B also on a short time scale; current PPFD significantly impacted K_B ($P < 0.001$) in 25-year-old silver birch trees grown in a natural forest stand. The shade shoots were more sensitive to small changes at low irradiance (70 to $140 \mu\text{mol m}^{-2} \text{s}^{-1}$) than sun shoots: K_B increased by 51% in the shade shoots and 26% in the sun shoots when PPFD increased from 70 to $330 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 2 in **Paper IV**). Similar stimulation of hydraulic conductance in response to rising irradiance has been shown in herbaceous plants (Nardini et al., 2005) and different tree species (Tyree et al., 2005; Scoffoni et al., 2008; Voicu et al., 2008; Aasamaa et al., 2012). Developed in different environments, shade shoots have adapted to respond to small changes in light availability,

while sun shoots can react to changes in high irradiance. Also, light-induced enhancement of leaf hydraulic conductance (K_L) depends on irradiance (Nardini et al., 2005; Sellin et al., 2008). Analogically, sun leaves tend to be more sensitive to fast changes in high irradiance ($900\text{--}1000\ \mu\text{mol m}^{-2}\text{ s}^{-1}$) than shade leaves (Öunapuu-Pikas & Sellin, 2020). On a short time scale, K_L increases due to the changes in the extravascular compartment of leaves and this is attributable to the activation or expression of plasma membrane aquaporins (Cochard et al., 2007; Dayer et al., 2017). However, not in all species has a link between K_L and aquaporin expression been proved (Voicu et al., 2009; Ben Baaziz et al., 2012).

In addition to light intensity, also light quality affects hydraulic conductance in silver birch (Table 1 in **Paper III**). Leaf-blade hydraulic conductance (K_{lb}) was highest in blue light, followed by white light, and lowest in red light. Under blue light, K_{lb} was on average 1.2 times higher than under white and 1.4 times higher than under red light (Figure 1 in **Paper III**), indicating that blue light with an emission maximum at 450–460 nm has a greater enhancing effect on leaf hydraulic conductance than white or red light. In bur oak (*Quercus macrocarpa* Michx.), K_L also increased under blue and green light compared to other wavelengths (Voicu et al., 2008). In five temperate deciduous tree species, low-irradiance blue light increased shoot hydraulic conductance (K_S) to the same extent as a very high irradiance of white light and more than a considerably higher irradiance of red light (Aasamaa et al., 2012). In the absence of blue spectral band, K_L may be up to 60% lower (Ben Baaziz et al., 2012). Blue light also increases palisade parenchyma and leaf total thickness, and enhances leaf photosynthetic quantum efficiency (Φ_{PSII} ; Zheng & Van Labeke, 2017). Thicker leaves and thicker palisade parenchyma result in better light absorption and higher photosynthetic capacity (Hanba et al., 2002). Many genes and proteins like auxin- and gibberellin-related genes, photosynthesis- and cryptochromes-related genes, and chlorophyll a/b binding protein are upregulated under blue light (Ren et al., 2020). Therefore blue light has a greater enhancing effect on leaf hydraulic capacity than white or red light. K_L is controlled through light-induced changes in membrane permeability of either mesophyll or bundle-sheath cells (BSC; Tyerman et al., 2002; Voicu et al., 2008; Grunwald et al., 2021a). It has been proposed that blue light controls leaf hydraulic conductance via the BSC blue light PHOT receptors, which activate the BSCs AHA2 H^+ -pump via an autonomous signaling pathway (Grunwald et al., 2021a).

In the plant hydraulic pathway, stems do not represent the major source of resistance. Much more resistance is located in shoots in the branch termini (Brodersen et al., 2019). Most of the shoot resistance in the hydraulic pathway is positioned in leaf blades (Figure 2 in **Paper III**). At least a third of the whole resistance to water flow within the plant is attributable to leaf tissues (Sack & Holbrook, 2006; Prado & Maurel, 2013). We saw a considerable redistribution of the liquid-phase resistance within the sample shoots in response to different light wavelengths. The leaf blades' role in the whole-shoot resistance increased, and bare branch resistance decreased from blue, white to red light in sun and shade

shoots (Figure 2 in **Paper III**). Hydraulic resistance in leaf vascular and extra-vascular compartments is principally of a similar magnitude (Sack & Holbrook, 2006). We also recorded changes in the distribution of hydraulic resistance on the circadian scale (Figure 4 in **Paper I**). In the morning, leaf blade resistance starts to decrease primarily with increasing blue light. The changes in distribution of hydraulic resistance with blue, white and red light support the idea that spectrum-sensitive light receptors are involved in the regulation of aquaporins (AQPs) in the bundle sheath and mesophyll cells (Ben Baaziz et al., 2012). AQPs play a central role in regulating plant water relations (Prado & Maurel, 2013; Chaumont & Tyerman, 2014; Maurel et al., 2015) because 95% of water movement through the plant plasma membrane is attributable to AQPs (Maurel et al., 2008). In walnut (*Juglans regia* L.), light-induced K_L is related to PIP1 and PIP2 aquaporin gene expression, but in beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.), only to PIP1 aquaporins (Ben Baaziz et al., 2012). One has to keep in mind that changes in the proportion of liquid-phase resistance allocated to leaves and branches reflects an overall hydraulic system adjustment to various environmental conditions, including temperature, wind, air humidity, and water availability.

Most of the studies on circadian patterns of trees' hydraulic traits have been performed in laboratory conditions (Zwieniecki & Holbrook, 1998; Bucci et al., 2003; Brodribb & Holbrook, 2004; Lo Gullo et al., 2005; Voicu et al., 2008; Cordeiro et al., 2009; Johnson et al., 2009; Locke & Ort, 2015). Less studies have investigated this topic in natural conditions (Bucci et al., 2003; Brodribb & Holbrook, 2004; Johnson et al., 2009, 2011; Yang et al., 2012; Öunapuu & Sellin, 2013). The hydraulic properties of hybrid aspen exhibited pronounced circadian patterns. Whole-branch hydraulic conductance (K_{wb} ; Figure 2), leaf-blade hydraulic conductance (K_{lb}), and petiole hydraulic conductance (K_P) varied significantly throughout the day (for all $P \leq 0.001$), but bare branch hydraulic conductance (K_B) did not (Figure 3 in **Paper I**). Hydraulic conductance started to rise slightly after midnight, and the process accelerated substantially in the morning, after sunrise. K_{wb} , K_{lb} and K_P reached their maxima between 9 and 12 h; afterwards, they gradually decreased. Plant species exhibit different circadian patterns of hydraulic traits (Lo Gullo et al., 2005; Johnson et al., 2009, 2011). Plant total hydraulic conductance often increases in the morning and achieves its maximum during the warmest hours of the day when evaporative demand is highest, as observed in silver birch (Öunapuu & Sellin, 2013), mahogany (*Swietenia macrophylla* King; Cordeiro et al., 2009) and in Mediterranean evergreens trees – *Ceratonia siliqua* L., *Olea europaea* L. and *Laurus nobilis* L. (Trifilò et al., 2014).

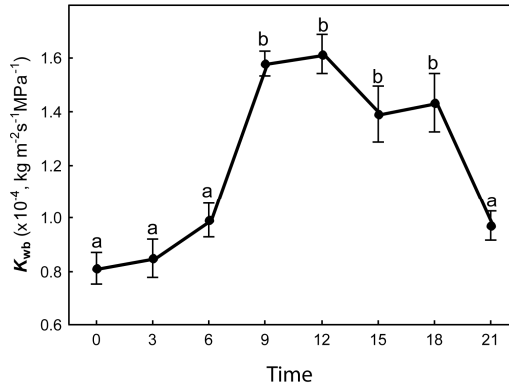


Figure 2. Daily dynamics of hydraulic conductance of whole branch (K_{wb}) in hybrid aspen. The vertical bars indicate \pm SE of the means.

Midday increase of K_L may be caused by aquaporin expression and/or activation (Lo Gullo et al., 2005; Chaumont & Tyerman, 2014). However, K_L may also be highest after dawn and may then decrease gradually (Lo Gullo et al., 2005; Voicu et al., 2008) or display a gradual increase from the morning to the late afternoon (Öunapuu & Sellin, 2013). A midday decline in K_L and K_P has been reported for many species (Bucci et al., 2003; Brodribb & Holbrook, 2004; Johnson et al., 2009; Yang et al., 2012; Locke & Ort, 2015). This pattern is typical for water-stressed plants (Bucci et al., 2003; Brodribb & Holbrook, 2006; Cordeiro et al., 2009) and may also occur in temperate species, with the decline of K_L being 15–66% (Johnson et al., 2009). The midday hydraulic decline is caused by decreased leaf water status and embolism formation, and it is generally repaired in the afternoon (Bucci et al., 2003; Brodribb & Holbrook, 2004; Johnson et al., 2009; Locke & Ort, 2015), but the recovery can take place also during the night (Yang et al., 2012; Trifilò et al., 2015).

The circadian patterns of hydraulic traits in aspen trees depend strongly on atmospheric conditions that determine water losses from the foliage. K_{wb} , K_{lb} , and K_P were positively correlated with photosynthetic photon flux density (PPFD), atmospheric vapour pressure deficit (VPD), air temperature (T_A), and negatively with relative air humidity (RH; **Paper I**). Similar relationships between hydraulic traits and atmospheric conditions have been shown for silver birch (Öunapuu & Sellin, 2013). A positive correlation between K_L and PPFD has been reported also for other deciduous and evergreen trees (Lo Gullo et al., 2005). K_B of aspen trees at the FAHM site (**Paper I**) was affected only by atmospheric evaporative demand (AED), but not by irradiance. The leafless branch does not have light-sensing systems. However, stems and branches have to provide an adequate water supply to the leaves, and their hydraulic capacity is modulated through other means. The hydraulic properties of hybrid aspen were primarily affected by air temperature (Table 2 in **Paper I**). In silver birch, T_A has the strongest effect, along with RH, on K_L (Öunapuu & Sellin, 2013). Due to the dual effect, temperature has a considerable influence on plant hydraulics on a daily scale: low temperatures decrease

plant hydraulic capacity (Cochard et al., 2000b; Ribeiro et al., 2009), while higher temperatures raise it (Matzner & Comstock, 2001; Sellin & Kupper, 2007). Indeed, temperature has been shown to be the primary explanatory variable of changes in K_L (Sellin & Kupper, 2007), but the temperature effects cannot be explained by changes in the water viscosity alone (Sack et al., 2004). Protoplast permeability has also been shown to be involved in temperature effects on K_L (Sellin & Kupper, 2007). All studied atmospheric factors (T_A , PPFD, RH and VPD) drove the hydraulic conductance of hybrid aspen. As these factors are inter-related, the differences in their significance were small. Our result suggests that a combination of different atmospheric characteristics, rather than one prevailing factor, shapes the circadian patterns of trees' hydraulic properties in natural environments.

We did not establish any statistically significant effects of air humidity manipulation on the hydraulic properties of silver birch (**Paper IV**). Nevertheless, the impact of the humidification treatment has been detected on various traits, such as tree gas exchange, root characteristics, growth rate, nutrient status, but also on some hydraulic and anatomical characteristics (Sellin et al., 2013; Parts et al., 2013; Tullus et al., 2014; Aasamaa et al., 2014; Lihavainen et al., 2016; Sellin et al., 2017b; Oksanen et al., 2019; Sellin et al., 2019; Rosenvald et al., 2021). In silver birch, leaf blade hydraulic conductance (K_{lb} ; $P = 0.023$) and petiole conductivity ($P = 0.046$) decreased in humified plots compared to control plots, which results from the declined transpirational flux and lower demand for transport capabilities (Sellin et al., 2013, 2019). Reduction in hydraulic efficiency in laminae and petioles of these trees is primarily attributable to changes in vessel size (Sellin et al., 2019). As for stem xylem, increasing air humidity influences its hydraulic efficiency, but not the functional vulnerability, in hybrid aspen (Sellin et al., 2017b). Humidification treatment increased wood density and decreased leaf area, leading to 34% higher average Huber values in humified plots compared to the control (Sellin et al., 2017b). Our previous studies (Sellin et al., 2013, 2017a, 2019; Tullus et al., 2014) suggest that the impact of elevated air humidity on plant hydraulic properties is complex and depends largely on the weather conditions prevailing during the growing period. Rainy summers (like 2009) and consequent low humidification efficiency could be the reason why we did not find significant treatment effects on hydraulic properties. This finding indicates the relatively conservative nature of the wood anatomical structure in silver birch. The same has been reported for hybrid aspen. The increasing atmospheric humidity predicted for higher latitudes leads to modest changes in the structure and functioning of the hybrid aspen xylem (Jasińska et al., 2015).

3.3. Relationships between hydraulic and xylem sap properties

We established a fair relationship between K_B and $[K^+]$ in hydraulically sampled branches of silver birch ($R^2 = 0.917$, $P = 0.003$; Figure 5 in **Paper IV** and $R^2 = 0.281$, $P < 0.05$, **Paper III**). In hybrid aspen, branch hydraulic properties were modulated by the ionic content of the xylem sap: K_{wb} , K_{lb} , and K_P depended on σ_{sap} and $[K^+]$ (Figure 3; Table 3 in **Paper I**), while the upregulation of branch hydraulic conductance in the morning (from 3 to 9 h) was strongly correlated ($R^2 = 0.940$, $P = 0.001$) with $[K^+]$. A strong positive relationship between mean values of hydraulic conductance of bare branches (K_B) and $[K^+]$ has also been found for silver birch (Sellin et al., 2013). The relationship depicted in Figure 3 is meaningful as it proves the role of ions (with the prevalence of K^+) in the up-regulation of K_L . These significant relationships between the hydraulic properties and $[K^+]$ of the xylem sap evidence that potassium ions are involved in regulating the hydraulic efficiency of both stems and leaves. It has been shown that the ionic effect is biggest under low ion concentrations (0–10 mM; van Ieperen and van Gelder, 2006; Zwieniecki et al., 2001). Overall, the ionic effect is species-specific and varies among different species and environmental conditions (Boyce et al., 2004; Jansen et al., 2011; Nardini et al., 2011b).

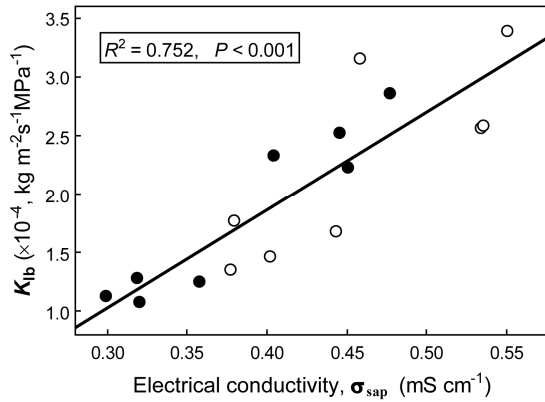


Figure 3. Mean electrical conductivity of xylem sap (σ_{sap}) versus leaf blade hydraulic conductance (K_{lb}) in hybrid aspen; $n = 16$. The data has been divided into two groups according to soil water potential at 30 cm depth (empty circles $\Psi_{S30} > -0.53$ kPa; filled circles $\Psi_{S30} < -0.53$ kPa).

The presence of K^+ in the perfused solution increased the hydraulic conductivity of branch xylem in aspen saplings by 31–35% compared to deionized water (Figure 4, unpublished data). For laurel plants, an increase of xylem hydraulic conductivity by ~30%, due to the ionic effect, has been reported (Gascó et al., 2006; Nardini et al., 2010). Replacing deionized water with ion solution in experiments may increase stem hydraulic conductance up to 58%, but it varies considerably

among species (Nardini et al., 2011b; Scoffoni et al., 2017). Nardini et al. (2011b) showed that stem hydraulic conductance increased on average by 17.1% among 35 angiosperm species. The ionic effect on xylem conductivity ranged from 1.9% in *Quercus ilex* to 58% in *Tilia platyphyllos*. Only five species out of 35 showed a conductivity enhancement of less than 5% (Nardini et al., 2011b).

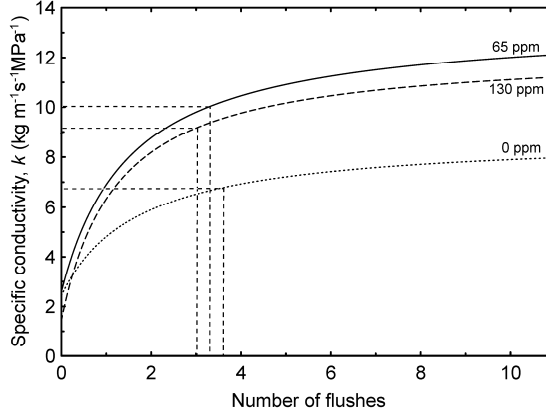


Figure 4. The effect of water saturation level on specific conductivity of the xylem (k) in hybrid aspen perfused with solutions differing in potassium ion concentration, fit using equation (7): $R^2=0.28$, $P<0.001$ for $[K^+]=0$ ppm; $R^2=0.41$, $P<0.001$ for $[K^+]=65$ ppm; $R^2=0.47$, $P<0.001$ for $[K^+]=130$ ppm (unpublished data). Before measurements, embolism of the stem segments was artificially induced by the air-injection technique, applying a pressure of 2.0 MPa for one hour. The dashed lines mark the specific conductivity at 75% water saturation.

A strong ionic effect and an efficient long-distance water transport system are vital preconditions in changing and spatially heterogeneous environmental conditions for hybrid aspen, a fast-growing tree species with near-anisohydric behaviour (Aasamaa et al., 2014; Sellin et al., 2017b; Kupper et al., 2018). In addition, at the leaf level, adequate water supply under high AED may be aggravated because of the lack of definite coordination between leaf hydraulic and stomatal traits (Sellin et al., 2021) and the low hydraulic plasticity of aspen leaves (E. Öunapuu-Pikas, unpubl.). Jansen et al. (2011) demonstrated a positive correlation between ionic effect and vessel grouping parameters, especially the portion of vessel walls being in contact with neighbouring vessels. Thus, the strong ionic effect in hybrid aspen can be explained by high intervessel connectivity: vessel grouping index is 1.65–1.70 and pitfield fraction is 68–71% (Jasińska et al., 2015). These values lie at the upper end of the ranges of both parameters published for a number of woody species from different families (Jansen et al., 2011; Nardini et al., 2012). In addition, the strong ionic effect observed in our experiment may be associated with high PLC, since Gascó et al. (2006) demonstrated an exponential increase of ionic effect in stems of *L. nobilis* with increasing PLC, compared with fully hydrated stems. Therefore, usually a higher ion-mediated increase in hydraulic efficiency

occurs in embolized stems than in fully hydrated stems (Gascó et al., 2006; Nardini et al., 2007). The substantial ion-mediated increase in hydraulic conductance suggests that adjusting the ionic content in xylem sap plays an essential role in modulating xylem hydraulic properties to meet environment-driven demand for foliage water supply.

The physico-chemical properties of xylem sap and branch hydraulic traits demonstrate coordinated circadian rhythms in hybrid aspens growing in their natural environment (**Paper I**). The branch hydraulic properties depend on the ionic content of the xylem sap (Figure 3; Table 3 in **Paper I**), but atmospheric variables may mask this effect on a circadian scale (Table 2 in **Paper I**). Direct impact of environmental conditions tends to outweigh the effects of xylem sap ionic content because the first is mediated by several other mechanisms (aquaporin activation, viscosity effects, stomatal regulation, etc.). Still, we observed a significant positive relationship between means of branch xylem sap $[K^+]$ and K_{wb} ($R^2 = 0.333$, $P = 0.019$) and K_{lb} ($R^2 = 0.370$, $P = 0.012$). An even stronger relationship occurred between σ_{sap} and K_{wb} ($R^2 = 0.740$, $P < 0.001$) and K_{lb} ($R^2 = 0.752$, $P < 0.001$; Figure 3).

Initial hydraulic conductivity (k_{in}) of branch segments of hybrid aspen after artificial embolism induction was related to maximum specific conductivity (k_{max}): k_{in} of the embolised sample increased with k_{max} ($R^2 = 0.177$, $P = 0.012$). k_{in} depended on neither air humidity treatment nor $[K^+]$. However, the presence of potassium ions enhanced the initial rate of recovery from cavitation, evidenced by the initial slopes of the response curves (Figure 4, unpublished data). K^+ accelerates embolism recovery, as the 50% saturation was achieved 19% faster and the 75% saturation 7–15% faster in branch segments perfused with KCl solution, compared to branch segments flushed with deionized water. Moreover, potassium ions may promote compensation for embolism-induced loss of conductivity through ion-mediated enhancement of radial water transport capacity through still functioning conduits (Trifilò et al., 2008, 2011). Higher potassium content in xylem sap might reduce the cavitation-induced loss of stem hydraulic conductivity through the enhancement of residual conductivity (Trifilò et al., 2008, 2011, 2014). Native $[K^+]$ is usually higher during the summer, the warmest hours of a day, and in water stress conditions when embolism occurs (Trifilò et al., 2008, 2011, 2014). In hybrid aspen saplings, native embolism increased from 16–20%, measured in the morning, to 36–41% around midday on summer days (Sellin et al., 2017b). $[K^+]$ follows the same daily course, responding to decreasing RH (**Paper I**). $[K^+]$ and osmolality (Osm) increase, along with rising cavitation in water stress conditions (Tyree et al., 1999). The relationship between hydraulic traits and Osm turned out to be weaker than that with $[K^+]$ and σ_{sap} (**Paper I**). That indicates that charged particles, rather than total solute content, in the xylem sap is responsible for the short-term modulation of xylem hydraulic conductance in trees.

3.4. Impact of phloem girdling on branch hydraulic conductance and physico-chemical properties of xylem sap

Our experiment on phloem girdling at the branch base resulted in a decline in stomatal conductance (g_s), net photosynthetic rate (P_N), leaf hydraulic efficiency, and in an increase of leaf water potential (Ψ_L) in hybrid aspen (Figures 1, 3 and 4 in **Paper II**). K_L of girdled branches decreased about 43% over 3 days after the girdling ($P = 0.006$; Figure 5 in **Paper II**). Domec and Pruyn (2008) indicated that a decline in transpiration causes a rapid decrease in K_L in response to girdling and might be explained by changes in leaf symplastic compartment and cell membrane AQP regulation. Changes in transpirational flux induce coordinated up/down-regulation of many aquaporin genes in leaves (Levin et al., 2007; Kuwagata et al., 2012). Besides, one cannot exclude the potential influence of mechanical injury, which may induce the blocking of vessels by pectin-like polysaccharides (Tyree & Zimmermann, 2013), lipid substances (Nemec, 1975), or water-soluble proteins (Neumann et al., 2010), reducing the hydraulic conductance. Altogether, a decline in K_L may result from changes in transpiration rate (E) and/or driving forces ($\Delta\Psi$; Figure 5 in **Paper II**). E declined due to the girdling ~39% over three days in our experiment (Table 2). A significant reduction in E due to phloem girdling has also been reported for coniferous trees like the Canary Island pine (*Pinus canariensis* C.Sm. ex D.C; López et al., 2015) and ponderosa pine (*Pinus ponderosa* Dougl. ex Law.; Domec & Pruyn, 2008). Reduced g_s and E resulted in higher leaf water potential (Ψ_L) in girdled branches (Figure 4 in **Paper II**). Similar response – high Ψ_L due to declined transpiration caused by phloem disruption – has also been described in grapevines (*Vitis vinifera* L.; Williams et al., 2000) and ponderosa pine (Domec & Pruyn, 2008). At the same time, we did not detect any differences in branch water potential (Ψ_B) between the control and girdled branches. The decline in g_s as a result of girdling is a common response observed in grapevines (Williams et al., 2000), olives (Annabi et al., 2019) and soybean (*Glycine max* cv. Siverka) plants (Castro et al., 2019). The decline in g_s may be generated by abscisic acid (ABA; Thomas & Eamus, 2002; Castro et al., 2019) or carbohydrate accumulation in leaves (Urban & Alphonsout, 2007; Domec & Pruyn, 2008). Branch girdling reduces sink demand and leads to sugar, starch, and ABA accumulation in leaves (Murakami et al., 2008; Rivas et al., 2011; Annabi et al., 2019; Castro et al., 2019). It also affects photosynthesis by reducing the quantum yield efficiency of photosystem II through feedback loops (Rivas et al., 2007; Urban & Alphonsout, 2007). We saw a fair coordination between gas exchange parameters and hydraulic efficiency in girdled branches ($R^2 = 0.295 - 0.441$, $P < 0.001$).

Table 2. Mean values of the physico-chemical properties of xylem sap and basic water relations parameters in hybrid aspen branches. $[K^+]$ – xylem sap potassium ion concentration; σ_{sap} – electrical conductivity; pH – xylem sap acidity; K_L – leaf hydraulic conductance; Ψ_L – leaf water potential; Ψ_B – branch xylem water potential; E – transpiration rate; g_s – stomatal conductance.

Variable	Mean		<i>P</i> -value
	Control	Girdled	
$[K^+]$ (mM)	0.44	0.65	0.180
σ_{sap} (mS cm ⁻¹)	0.59	0.64	0.557
pH	6.3	6.5	0.185
K_L (mmol m ⁻² s ⁻¹ MPa ⁻¹)	6.64	3.78	0.006
Ψ_L (MPa)	-1.19	-0.67	0.002
Ψ_B (MPa)	-0.47	-0.45	0.900
E (mmol m ⁻² s ⁻¹)	4.66	0.61	<0.001
g_s (mol m ⁻² s ⁻¹)	0.454	0.078	<0.001

The phloem girdling experiment indicated that the decline in K_L was not associated with xylem sap ionic content in hybrid aspen. It has been reported that phloem girdling reduces branch xylem hydraulic conductance and osmotic concentration of the xylem sap simultaneously in two *Acer* species (Zwieniecki et al., 2004). Girdling induced a decrease of $[K^+]$ of the xylem sap also in *Diospyros kaki* stems (Fumuro, 1998). Stem girdling also inhibits refilling of the embolized vessels (Salleo et al., 2004), which depends on xylem sap ionic content (Gascó et al., 2006; Trifilò et al., 2008, 2011, 2014). Ions are released into the stem xylem from living tissues like the phloem (De Boer & Volkov, 2003; Zwieniecki et al., 2004), through which xylem and phloem functioning are partly coupled (Konrad et al., 2019). Zwieniecki et al. (2004) explain that phloem girdling leads to a decrease of ion concentration in xylem sap because it disturbs the ion exchange between phloem and xylem. Our results did not support this mechanism. The decline in K_L (Table 2) was not accompanied by changes in $[K^+]$, σ_{sap} , or pH of the xylem sap in hybrid aspen trees. Thus, the phloem girdling at branch base did not significantly impact those xylem sap properties in hybrid aspen. A similar finding has been reported for laurel plants (Nardini et al., 2010). The girdled branch remained connected with the tree, and only a tiny part of the phloem was removed. Lateral transport between phloem and xylem could still occur in other parts of the tree, and ions could have been transported from other parts to the manipulated branch. That can explain why we did not find changes in the xylem sap properties between control and girdled branches. As potassium recirculates between the xylem and phloem (Holbrook & Zwieniecki, 2011), the xylem sap $[K^+]$ may be enhanced due to the recirculation (Metzner et al., 2010) and this helps to avoid cavitation and cope with embolism (Gascó et al., 2006; Trifilò et al., 2011). The mechanism of how girdling affects ion recirculation between phloem and xylem, and the hydraulic conductance of plants needs further investigation.

4. CONCLUSIONS

Water transfer from roots to leaves is essential for plants in order to keep up photosynthesis, to grow and survive. Water transport capacity in fast-growing broad-leaved trees like silver birch and hybrid aspen is modulated by xylem sap ionic content – increased xylem sap potassium ion concentration ($[K^+]$) promotes trees' hydraulic capacity (**Papers I and IV**). The significant relationships observed between hydraulic conductance and $[K^+]$ of the xylem sap indicate involvement of potassium ions in the regulation of xylem hydraulic efficiency in response to changes in the environment. In addition, potassium ions may compensate for the embolism-induced loss of conductivity through ion-mediated enhancement of lateral movement of water.

Both xylem hydraulic properties and the physico-chemical properties of xylem sap in trees follow circadian patterns driven by environmental conditions. They exhibit coordinated circadian rhythms in hybrid aspens growing in their natural environment: a significant increase in the morning, with rising sunlight; their maxima are achieved during the warmest hours of the day, when evaporative demand is highest, after which hydraulic conductance and xylem sap ionic content start to decrease. The enhancement of branch hydraulic conductance in the morning and in response to growing evaporative demand is associated with the upregulation of potassium ion concentration in the xylem sap. Solid correspondence between leaf-blade hydraulic conductance, $[K^+]$, and electrical conductivity of xylem sap suggests that leaf hydraulic efficiency can also be tuned by adjusting sap ionic strength (**Paper I**).

Daily dynamics of xylem sap $[K^+]$ depends significantly on both soil water status and atmospheric conditions. Hydraulic properties of branches and leaves are driven by atmospheric evaporative demand (T_A , RH and VPD) and irradiance, indicating that different environmental characteristics, combined, shape the circadian patterns of trees' hydraulic traits in natural habitats. In uncontrolled field conditions, highly variable atmospheric factors tend to mask the ionic effect: the direct impact of environmental conditions on plant hydraulic efficiency outweighs that of xylem sap properties (**Paper I**).

Phloem transport disruption by phloem girdling at branch base in hybrid aspen reduces transpiration, stomatal conductance, net photosynthetic rate, and leaf hydraulic conductance, and increases leaf water potential. At the same time, it does not affect xylem sap $[K^+]$, electrical conductivity, and pH, indicating that lateral transport of ions is not disturbed by the girdling manipulation. The decline in leaf hydraulic conductance in response to the manipulation is associated with diminished transpirational flux and consequent changes in leaf symplastic compartment, rather than with shifts in xylem sap ionic contents (**Paper II**).

Branch hydraulic conductance and xylem sap ionic content increase from the bottom to the top of the crown. Sun-exposed branches exhibit higher hydraulic conductance and xylem sap $[K^+]$ than shade shoots, in order to provide adequate water supply to the foliage experiencing higher water loss. Moreover, upper-

canopy leaves commonly exhibit less water saving behaviour, which may be beneficial for the fast-growing pioneer species on a daily basis. Shade-acclimated shoots, in contrast, are more sensitive to small changes at low radiation levels compared to sun shoots. The current study provides experimental evidence for light-mediated changes of stem hydraulic conductance in field-grown plants. This effect is supported by adjustment of $[K^+]$ in xylem sap depending on light availability (**Paper IV**).

Hydraulic conductance is considerably affected by light quality, independently of light intensity or total light energy received (**Paper III**). Blue light has a significant enhancing effect on leaf hydraulic conductance (K_L) compared to white or red light, suggesting that spectrum-sensitive light receptors are involved in the regulation of aquaporins in the bundle sheath and mesophyll cells. Spectral gradients existing within natural forest stands represent signals for the fine-tuning of tree water relations to afford lavish water use in sun foliage and limit the water use of shade foliage, sustaining greater hydraulic constraints. Given that natural plant canopy depletes blue and red light, K_L is probably decreased within the canopy both by reduced irradiance and shifts in light spectra. Due to the differential sensitivity of K_L to the light spectrum, spatial and temporal variation in light quality contributes to the (re)distribution of hydraulic resistance within trees in response to changing conditions inside forest canopies.

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SUMMARY IN ESTONIAN

Ksüleemimahla kaaliumioonide sisalduse ja valgustingimuste mõju puude hüdraulilistele omadustele

Vee transport juurtest lehtedesse on taimede ellujäämiseks ülioluline, kuna mõjutab taimede võimet assimileerida süsiniku ja täita teisi elutähtsaid funktsioone. Ksüleemi hüdrauliline juhtivus mõjutab transpiratsiooni, lehe veetranspordivõimet, õhulõhede juhtivust, fotosünteesi ja puu produktiivsust. Vee kaugtranspordi käivitavaks jõuks on transpiratsioon – vee pidev aurumine lehepinnalt, mis kohesiooniteooria kohaselt tõmbab veesammaste kaudu vett mullast lehtedesse. Peamiselt liigub vesi juurtest lehtedesse mööda trahheedest ja trahheidiidest koosnevat ksüleemi, mille anatoomiast hüdrauliline juhtivus otseselt sõltub. Tulenevalt Hagen-Poiseuille' seadusest juhivad suure diameetriga trahheed paremini vett kui kitsad trahheed ja trahheiidid, kuna kapillaari teoreetiline hüdrauliline juhtivus on võrdeline tema raadiuse neljanda astmega. Samas on suured trahheed tundlikumad kuivastressile ja kaviteeruvad kergemini. Traditsiooniliste arusaamade kohaselt määravad soontaimede ksüleemi hüdraulilise juhtivuse üksnes anatoomilise ehituse iseärasused ja juhtkoe veega küllastatuse tase, kuid 21. sajandi alguses avastati, et lisaks mõjutab hüdraulilist juhtivust ka ksüleemimahla ionide sisaldus. Seega ei saa ksüleemi veetranspordi käsitleda täielikult passiivse protsessina.

Doktoritöö käsitleb ksüleemimahla ionide sisalduse, valgustingimuste mõju ja hüdraulika omavahelisi seoseid kiirekasvulistel lehtpuudel. Täpsemalt uurisin:

- hüdrauliliste ja ksüleemimahla füüsikalis-keemiliste parameetrite ööpäevast dünaamikat (I)
- floemi salkamise mõju hüdraulilise juhtivusele ja ksüleemimahla ionide sisaldusele (II)
- valguse kvaliteedi ja intensiivsuse mõju lehe ja oksa hüdraulilisele juhtivusele (III ja IV).

Uuringud tegin Tartu maakonnas looduslikult uuenenud segametsas Järvelja Õppe- ja Katsemetskonna maadel ning Kastre vallas Rõkal asuval metsaökosüsteemi õhuniiskuse manipuleerimise katsealal (FAHM). Uurimisobjektideks olid kiirekasvulised heitlehised puud: hübriidhaab (*Populus tremula* L. × *P. tremuloides* Michx.) ja arukask (*Betula pendula* Roth). Hüdrauliliste parameetrite mõõtmiseks kasutasin kahte erinevat meetodit – evaporatiivse voo ja kõrgsurve meetodit.

Töös tõestasin ksüleemimahla ionide sisalduse mõju katsealuste liikide hüdraulilisele juhtivusele. Nii hübriidhaaval kui ka arukasel korreleerus ksüleemimahla ionide sisaldus puidu hüdraulilise juhtivusega. Suurenenud ksüleemimahla K^+ sisaldus suurendab hüdraulilist juhtivust, viidates K^+ osalusele taimede

veevahetuse regulatsioonis. Ioonide kontsentratsioonist sõltuvad ksüleemi hüdraulilise juhtivuse muutused on tingitud ksüleemirakkude-vaheliste koobaspooride membraanidel asuva pektiinmaatriksi paisumisest ja kokkutõmbumisest, kuna pektiini maatriks reageerib ionide sisaldusele ksüleemimahlas. Selle täpne mehhanism on seni veel teadmata. Lisaks kiirendab ksüleemimahla K^+ sisaldus kavitatsioonist taastumist, kuna kaalium soodustab vee lateraalsuunalist transporti trahheede ja trahheiidide vahel. Ksüleemimahla kõrge ionide sisaldus võib soodustada katkenud veesammaste taastumist ksüleemis ja seeläbi vähendada embolismist tingitud veetranspordi vähenemist.

Puude hüdraulilist juhtivust iseloomustab teatud ööpäevane dünaamika. Hübriidhaava ksüleemimahla ionide sisalduse ja hüdrauliline juhtivuse ööpäevased rütmid on koordineeritud – hommikul päikesetõusuga mõlemad suurenevad, saavutavad maksimumi keskpäeva paiku või natuke pärast seda, kui aurumine lehepinnalt ja veenõudlus on kõige suuremad. Seejärel hakkavad mõlemad aeglaselt vähenema. Selline ööpäevane dünaamika on iseloomulik parasiiskete koosluste puudele, kus vesi ei ole limiteerivaks faktoriks. Kuivastressi korral puude keskpäevane hüdraulilise juhtivus väheneb oluliselt, millest taastumine toimub kas pärastlõunal või öösel. Valguse intensiivsus ja atmosfääri-faktorid mõjutasid oluliselt nii hübriidhaava hüdraulikat kui ka ksüleemimahla omadusi, ent atmosfäärifaktorite (fotosünteesiliselt aktiivse kiirgusvoo tihedus, õhutemperatuur, suhteline õhuniiskus, atmosfääri veeaururõhu defitsiit) suur varieeruvus varjutas hübriidhaava ksüleemimahla ionide sisalduse mõju hüdraulilisele juhtivusele. Lehelaba, leherootsude ja kogu oksa hüdrauliline juhtivus sõltusid oluliselt kõigist mainitud keskkonnafaktoritest, kõige enam õhutemperatuurist. Oksa puitunud osa hüdrauliline juhtivus sõltus eelkõige atmosfääri evaporatiivsest nõudlusest (AED), kuid mitte valguse intensiivsusest. Ksüleemimahla ionide sisaldus sõltus aga mulla veesisaldusest (mulla veepotentsiaalst) ja atmosfääri nõudlusest. Mulla veesisaldus mõjutab vahetult ionide omastamise efektiivsust mullast. Tulemused kinnitavad, et keskkonnatingimused mõjutavad otseselt hübriidhaava hüdraulilist juhtivust ja ksüleemimahla parameetreid, kuid tegemist on erinevate faktorite koosmõjuga. Hüdraulilise efektiivsuse kiire reguleerimine vastavalt muutuvatele keskkonnatingimustele võimaldab taimedel maksimeerida süsiniku omastamist, mis on kiirekasvuliste liikide jaoks oluliseks funktsionaalseks tunnuseks.

Ksüleemimahla ionide sisaldus ja oksa hüdrauliline juhtivus suurenevad koordineeritult liikumisel võra aluselt ladva suunas. Võra ülaosas, valgusele hästi eksponeeritud okste K^+ sisaldus ja hüdraulilised parameetrid on oluliselt kõrgemad kui võra alaosas paiknevate varjuokste vastavad näitajad. Veetranspordi seiskohast on valgusoksad oluliselt efektiivsemad kui varjuoksad, kuna keskkonnatingimusest johtuvalt on valgusokstes ja eelkõige lehtedes juhtkoed tugevamini arenenud. Hüdrofiilsete transportvalkude – akvaporinide (AQP) – ekspressioon või aktivatsioon rakumembraanidel alandab takistust vee liikumisele lehe ekstravaskulaarsel teekonnal. Hüdraulilise juhtivuse ja ksüleemimahla K^+ sisalduse dünaamika ajaline kattuvus sõltuvalt valguse intensiivsusest viitab, et kaaliumioonid reguleerivad tüve hüdraulilist juhtivust, mis reageerib ka valguse

intensiivsuse muutustele. Võrreldes valgusvõrsetega on varjuvõrsed valguse muutustele tundlikumad väikeste kiirgustasemetega korral. Lisaks valguse intensiivsusele mõjutab hüdraulilist juhtivust ka valguse kvaliteet – sinine valgus stimuleerib lehtede hüdraulilist juhtivust oluliselt rohkem kui valge või punane valgus. Kuna lehed moodustavad väga suure osa (>30%) kogu puu hüdraulilisest takistusest, muudab erineva lainepikkusega valgus vedela faasi takistuse jaotust puudes. Valguse kvaliteet mõjutab hüdraulilist juhtivust läbi valgusretseptorite, mis osalevad akvaporinide ekspressioonis.

Floeemi sälkamine oksa alusel põhjustab hübriidhaaval transpiratsiooni, õhulõhede juhtivuse, fotosünteesi ja hüdraulilise juhtivuse drastilist langust ning lehe veepotentsiaali tõusu. Samas ei mõjutanud floeemitranspordi blokeerimine ksüleemimahla füüsikalise-keemilise omadusi – ei ksüleemimahla K^+ sisaldust, elektrilist juhtivust ega pH-d, viidates sellele, et ionide lateraalne transport ning nende retsirkulatsioon floeemi ja ksüleemi vahel ei ole hübriidhaaval floeemi sälkamisest mõjutatud. Järelikult ei saa ksüleemi hüdraulilise juhtivuse vähenemine sälgatud okstes võrreldes intaktsete okstega olla seotud ksüleemimahla katioonide sisaldusega, vaid sõltub pigem muutustest lehe sümplastes komponentides, mis on indutseeritud transpiratsioonivoo aeglustumisest. Täpsed mehhanismid, mis käivituvad floeemitranspordi häirumise tagajärjel, vajavad veel täiendavaid uuringuid.

Puude veetranspordisüsteemi ehitus ja funktsioneerimine mõjutavad oluliselt puude kasvu, konkurentsivõimet ja produktiivsust. Teadmised puude veevahetuse toimimisest ja seda mõjutavatest keskkonnateguritest aitavad meil ennustada puude kohanemisvõimet tuleviku kliimatingimustega ja mõista ökosüsteemide toimimist tervikuna.

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PUBLICATIONS

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Sellin, A.; Õunapuu, E.; **Karusion, A.** (2010). Experimental evidence supporting the concept of light-mediated modulation of stem hydraulic conductance. *Tree Physiology*, 30 (12), 1528–1535. 10.1093/treephys/tpq091
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- 2008** International Taiga Rescue Network Conference, Petrozavodsk, Venemaa (stendiettekanne)
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- 2017** XIX International Botanical Congress, Shenzhen, Hiina (suuline ettekanne)
- 2017** 3rd Xylem International Meeting, Bordeaux, Prantsusmaa (suuline ettekanne)
- 2018** International Conference on Climate Change & Water, Tours, Prantsusmaa (stendiettekanne)
- 2018** Multiscale Plant Vascular Biology: Knowns and Unknowns of Plant Vascular Responses to Environmental Change. Gordon Research Seminar, West Dover, USA (suuline ettekanne)
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