

OTT KANGUR

Nocturnal water relations and
predawn water potential disequilibrium
in temperate deciduous tree species



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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** **Kangur O**, Kupper, P, Sellin A. 2017. Predawn disequilibrium between soil and plant water potentials in light of climate trends predicted for northern Europe. *Regional Environmental Change* **17**: 2159–2168.
- II** **Kangur O**, Tullus, A, Sellin A. 2020. Night-time transpiration, predawn hydraulic conductance and water potential disequilibrium in hybrid aspen coppice. *Trees – Structure and Function* **34**: 133–141.
- III** Kupper P, Rohula-Okunev G, Sell M, **Kangur O**, Sellin A. 2020. Effects of air humidity and soil nitrogen source on diurnal water flux in hybrid aspen and silver birch. – In: Acta Horticulturae, ISHS (*accepted*).
- IV** **Kangur O**, Steppe K, Schreel JW, von der Crone JS, Sellin A. Variation in nocturnal stomatal conductance and development of predawn disequilibrium between soil and leaf water potentials in nine temperate deciduous tree species. *Manuscript submitted for publication*.

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

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

LIST OF ABBREVIATIONS

AED	atmospheric evaporative demand
E	transpiration (g h^{-1})
E_n	nocturnal transpiration (g h^{-1})
F	sap flux density ($\text{g m}^{-2} \text{h}^{-1}$; $\text{mmol m}^{-2} \text{s}^{-1}$)
F_n	nocturnal sap flux density ($\text{g m}^{-2} \text{h}^{-1}$; $\text{mmol m}^{-2} \text{s}^{-1}$)
FWU	foliar water uptake
g_d	daytime stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_{\min}	minimum leaf conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_n	nocturnal stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_{pd}	predawn stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
$g_{\text{pd_dry}}$	predawn stomatal conductance, soil water content < 25% ($\text{mmol m}^{-2} \text{s}^{-1}$)
$g_{\text{pd_wet}}$	predawn stomatal conductance, soil water content > 40% ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_s	stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
$K_{\text{S-L}}$	soil-to-leaf hydraulic conductance ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
PDD	water potential predawn disequilibrium (MPa)
Q_n	nocturnal sap flow (g h^{-1})
R_n	nocturnal tissue refilling (g h^{-1})
RH	relative air humidity (%)
SWC	volumetric soil water content (%)
T_a	air temperature ($^{\circ}\text{C}$)
VPD	atmospheric vapour pressure deficit (kPa)
Ψ	water potential (MPa)
Ψ_B	xylem water potential of branches (MPa)
Ψ_L	leaf water potential (MPa)
Ψ_{pd}	predawn leaf water potential (MPa)
Ψ_S	soil water potential (MPa)

1. INTRODUCTION

1.1. Trees' nocturnal water use

Most plant species have small pores called stomata on the leaf surface, through which prevailing part of gas exchange between the plant and the surrounding atmosphere takes place. Major fluxes through stomata are CO₂ diffusion into the plant and efflux of water vapour from the leaf. Optimization theory states that stomata should act to maximize carbon gain while minimizing water loss (Cowan and Farquhar 1977). According to that, plants should keep their stomata open during daytime to assimilate CO₂ – input for photosynthesis – and keep them closed during night-time to minimize the loss of water while there is no sunlight and photosynthesis is not possible. Nevertheless, it has been demonstrated that many plant species keep their stomata at least partially open at night (Caird et al. 2007; Zeppel et al. 2014; Kupper et al. 2018).

Stomatal openness is usually expressed as stomatal conductance (g_s , mmol m⁻² s⁻¹), the rate of passage of water vapour exiting the leaf through the stomata. The highest mean nocturnal stomatal conductance (g_n) values have been demonstrated by hemiparasites (~500 mmol m⁻² s⁻¹), but tropical tree species also demonstrate relatively high values (~100 mmol m⁻² s⁻¹). Relatively low values of g_n (mean ~25 mmol m⁻² s⁻¹) have been recorded in gymnosperm and evergreen angiosperm tree species (Resco de Dios et al. 2019). Consequently, g_n is highest in the tropics, and lowest in Mediterranean and boreal biomes, where it is approximately three times lower compared to the tropics (Resco de Dios et al. 2019). On average the ratio of g_n and daytime stomatal conductance (g_d) is highest (~0.5) in deserts, and lowest (~0.1) again in the Mediterranean biomes (Resco de Dios et al. 2019). However, g_n has been recorded to reach up to 90% of g_d (Caird et al. 2007).

Depending on atmospheric evaporative demand (AED) during the night, plants may lose a considerable amount of water as a result of nocturnal transpiration (E_n). However, as night-time AED is usually much lower than daytime AED, g_n is not reflected proportionally in nocturnal water losses (Caird et al. 2007). In many studies (Dawson et al. 2007; Scholz et al 2007; Sellin and Lubenets 2010; Alvarado-Barrientos et al. 2013) nocturnal sap flow has been used as a proxy of E_n . Respective measurements on various tree species from diverse habitats have shown that nocturnal water use on average makes up 10–15% of the total daily (24 h) transpiration (Forster 2014). One should consider that E_n usually constitutes less than 10–15% of the total daily transpiration, since part of the data obtained from sap flow measurements includes the refilling of the tissues that have been depleted during the daytime (Fisher et al. 2007).

Factors affecting g_n and E_n can roughly be divided into biotic and abiotic factors, but specific factors or the direction of their effect may vary between day- and night-time. For example, there is no reason to discuss the effect of incident radiation on g_n . Meanwhile, the effect of soil moisture and different atmospheric

conditions have been investigated in numerous experiments. Soil moisture has a similar effect on g_n and E_n as it has on the respective daytime values: moist soil improves leaf water status, which in turn favours higher stomatal conductance, and dry soil, on the contrary, causes stomata to close, which in turn reduces E_n (Zeppel et al. 2014). Therefore, the higher the soil moisture content, the higher the g_n and E_n , and *vice versa*. However, previous studies have only investigated the effect of soil moisture content on g_n in one or a couple of species at a time. So far, also the effect of soil oversaturated with water on g_n or on E_n has not been studied experimentally. Atmospheric vapour pressure deficit (VPD) is most often used to quantify AED: the higher VPD, the higher AED. It is a product of both air temperature and relative air humidity (RH). Based on current knowledge, the effect of VPD on g_n is controversial. Some studies have demonstrated a positive effect (Dawson et al. 2007; Zeppel et al. 2012) or no effect on g_n (Pfautsch et al. 2011). More studies have demonstrated a negative effect of VPD on g_n (Bucci et al. 2004; Christman et al. 2009; Ogle et al. 2012; O’Keefe and Nippert 2018) like it is commonly observed during daytime. Many studies have reported a strong positive relationship between VPD and nocturnal sap flow (Benyon 1999; Mitchell et al. 2009; Alvarado-Barrientos et al. 2013; Gotsch et al. 2014, Zeppel et al. 2014), but the majority of them have not measured actual E_n . According to some studies that have used nocturnal sap flow as an indirect estimate of E_n , wind speed possesses a positive effect on E_n (Benyon 1999; Sellin and Lubenets 2010; Kupper et al. 2018). It has also been shown that nocturnal water use depends on nutrient availability in the soil, however, the directions of the responses of plants could be different – in savanna trees, g_n and nocturnal sap flow were greater under nutrient deficiency (Scholz et al. 2007; Bucci et al. 2016), while hybrid aspen trees growing in fertilized soil exhibited greater nocturnal sap flow (Kupper et al. 2012).

Among biotic drivers, plant intrinsic factors have been studied, but much less than abiotic factors. It is known that younger leaves have weaker stomatal control than mature leaves and therefore g_n is usually higher in the former (Zeppel et al. 2010). In eucalypt trees, post-fire regrowth exhibits higher nocturnal sap flow compared to mature trees, which is probably related to overall higher stomatal conductance, including g_n , in regrowth (Buckley et al. 2012). Lower stomatal conductance in taller trees is related to sustaining leaf water status under burdens of water transport in tall trees (Delzon et al. 2004). Also, on the contrary, a young *Pinus patula* Schiede ex Schltdl. et Cham. stand demonstrated an approximately two-fold higher ratio of nocturnal to daily total water loss compared to a mature stand (Alvarado-Barrientos et al. 2013). In addition, fast-growing tree species tend to exhibit higher g_n or nocturnal transpiration rates compared to species with relatively slow growth (Daley and Phillips 2006; Marks and Lechowicz 2007; Howard and Donovan 2010).

It is important to acknowledge that g_n and E_n enhance water uptake by plants from the soil. That knowledge is essential for accurate assessment of water reserves in the soil. Previous land-surface models assessing water reserves assumed that plants keep their stomata closed at night and E_n is zero (Lombardozzi et al. 2017).

More recent models also take into account g_n and concomitant E_n , which has led to the understanding that globally the water loss due to E_n is 5% larger, in the tropics and in drier regions even ca 30% larger, than previously thought. That results in 10% lower soil water content in arid and semiarid ecosystems, in some regions even up to 50% lower available soil moisture (Lombardozzi et al. 2017). On the other hand, E_n prevents plant tissues to completely recharge with water by the beginning of the day (Donovan et al. 2001; Bucci et al. 2004). This means that in the morning or during midday, plant water status may drop to a level inducing stomatal closure earlier than without nocturnal water loss, to protect vascular tissues from hydraulic failure (Brodribb and Holbrook 2004). Early stomatal closure shortens the period when photosynthetic carbon acquisition can take place (Medrano et al. 2002).

1.2. Predawn water potential disequilibrium

Water potential (Ψ) is the measure of potential energy of water that drives the movement of water through plants. It is widely used to describe plant water status or the water status of a plant's particular part (e.g. leaf, branch) that is of interest. Ψ is usually expressed in pressure units (megapascal, MPa; kilopascal, kPa) and has a negative value, as it is expressed relative to pure water in reference conditions. The higher (i.e. the less negative) Ψ in a particular plant organ is, the closer to water saturated state that organ is and the more difficult it is for water to move into that organ. The lower (i.e. more negative) Ψ is, the further away from saturated state that part is and water can move towards that part more easily. Plant Ψ is mainly determined by environmental factors like soil water status, i.e. soil water potential (Ψ_s), and AED, i.e. VPD, and on the other hand by stomatal openness controlling transpiration from leaves. Additionally, solute concentration (i.e. osmotic component) in a plant and tree height (i.e. gravitational component) also affect Ψ (Kramer and Boyer 1995), but these components are not important in the context of the current thesis.

Ψ_s determines how well plants are supplied with water and basically also the maximum Ψ that could theoretically be reached in a plant. VPD and stomatal openness combined determine how much plants lose water. Plants exhibit the lowest Ψ under drought conditions when water movement to plants is hindered by low soil water availability. When soil water supply is sufficient, then the lowest Ψ in plants occurs around midday in sunny days, when VPD is the highest and stomata are wide open, which cause rapid loss of water from leaves. Plants exhibit the highest Ψ when soil water supply is adequate, i.e. Ψ_s does not limit plant water uptake, VPD is zero or close to it and stomata are completely closed and transpiration from leaves is negligible (Larcher 2003). Such a situation usually occurs at night. During that time plants refill their tissues with water that has been depleted during the daytime and, as a result, plants reach the highest Ψ values at the end of the night – at dawn.

For a long time, it was assumed that plants keep stomata tightly closed at night and as a result plant Ψ should equilibrate with that of the soil at predawn. That assumption has been widely used in ecophysiological studies (Drake and Franks 2003; Tramontini et al. 2013; Martinez-Vilalta et al. 2014; Zhang et al. 2019): for estimating Ψ_S one could measure predawn leaf water potential (Ψ_{pd}), as the latter should be equal to Ψ_S . However, considering the g_n and concomitant E_n that is observed in quite many species, Ψ_{pd} tends to be lower than it would be with completely closed stomata and therefore equilibration between Ψ_S and Ψ_{pd} cannot take place. In that situation Ψ_{pd} gives a biased estimation of Ψ_S . It has been demonstrated in woody species from the Brazilian tropical savanna, the North American cold desert and temperate forests that those species exhibit lower Ψ_{pd} than Ψ_S because of nocturnal transpiration (Donovan et al. 1999; 2003; Bucci et al. 2004; 2005; Kavanagh et al. 2007). The phenomenon when Ψ_{pd} does not equilibrate with Ψ_S is called water potential predawn disequilibrium (PDD; Donovan et al. 1999). In the case of open stomata, PDD should be larger with higher VPD, as transpirational water loss is highly dependent on atmospheric conditions.

Besides nocturnal transpiration there are other mechanisms that might contribute to PDD. The second one could be severe soil water deficit, which leads to weakened contact between root surface and soil solution, which in turn constrains the entering of water into the roots (Cochard et al. 1996). However, Ourcival and Berger (1995) found that the drier the soil became, the more equal Ψ_{pd} and Ψ_S became. The third mechanism is associated with plants' high capacitance and/or too short nights. Bucci et al. (2004) demonstrated that the period necessary to recharge large tropical savanna trees might be longer than the length of a night. At high latitudes, midsummer nights are very short, which may also prevent equilibrium between Ψ_{pd} and Ψ_S to be reached, as it was demonstrated for *Picea abies* (L.) H. Karst. and *Vaccinium myrtillus* L. (Sellin 1999). The fourth mechanism contributing to PDD could be hydraulic lift, which is more common in dry biomes. This phenomenon is caused by differences in Ψ_S between different soil layers. Water is absorbed by roots from deeper, wetter layers, but in upper dry layers water is passively sucked out from the roots, which partly constrains water reaching plant aboveground parts. Therefore, the aboveground tissues might not be refilled with water during night and equilibrium is not reached (Donovan et al. 1999). The fifth mechanism is associated with leaf apoplastic solutes. Some salt tolerant plant species accumulate salts in their apoplast in high concentrations, which, through changes in osmotic potential, lowers leaf water potential (Donovan et al. 2003). As a consequence, Ψ_{pd} might also remain significantly lower than Ψ_S .

Several studies (Dawson 1998; Limm et al. 2009; Eller et al. 2013; Hill et al. 2015) demonstrate that some plants are able to absorb water from the leaf surface, i.e. weather events making leaves wet (precipitation, fog, dew formation) can induce a phenomenon called foliar water uptake (FWU). On average, those events occur over 100 days a year across all ecoregions of the world (Dawson and Goldsmith 2018), making FWU potentially a very common mechanism across biomes (Schreel and Steppe 2020). FWU may improve plant water status and increase its photosynthetic capacity (Dawson and Goldsmith 2018). The water assimilated

through the leaves can release tension on the water column inside plants, enable turgor-driven growth, promote embolism repair and could delay the increased probability of reaching the critical or lethal water potential threshold leading to tree mortality (Schreel and Steppe 2019). As summer nights in Estonia are relatively cool and humid, which are good preconditions for dew formation, it is likely that deciduous trees growing here might also exhibit FWU, which in turn may influence predawn leaf water status and development of PDD.

1.3. Possible impact of climate change

Climate models predict that during the following decades various environmental conditions will change around the world. It is a universal trend that the average air temperature will rise in different regions (IPCC 2013). In most regions across low- and mid-latitude continental areas, that rise is coupled with a decrease in precipitation, which leads to drier soils and more frequent and extreme droughts. However, at higher latitudes in northern Europe and North America rain events will become heavier and more frequent. In northern Europe, annual precipitation since 1960 shows an increasing trend of up to 70 mm per decade and mean summer precipitation, up to 18 mm per decade (EEA 2017). In Estonia, during 1966–2015 the average summer precipitation increased by 12.3 mm per decade, and the trend was significant in June – the period of the fastest development of foliage (Jaagus et al. 2018). The models project an increase of up to 20–30% in summer precipitation for northern Europe by the end of the century (Scoccimarro et al. 2015). Relative air humidity (RH) remains approximately constant on climatological time scales and planetary space scales, implying a strong constraint by the Clausius–Clapeyron relationship on how specific humidity will change (O’Gorman and Muller 2010). However, RH increases due to rising amount and frequency of rainfalls on regional or local scales (Betts et al. 2014). On average, the climate in those regions will become more humid. This is particularly characteristic for forested areas, as mean interception rates for different tree species range 10–58% of the gross rainfall (Yang et al. 2004; Yang et al. 2019); from forest canopies water eventually evaporates back to the atmosphere, raising RH on a local scale. On the other hand, it is proposed that all kinds of extreme weather events will become more frequent and extreme (IPCC 2013). Thus, despite of the shift towards moister climate at higher latitudes, it is probable that drought events will also become more frequent and severe.

The aforementioned changes in environmental conditions should have an impact on plant water relations, including nocturnal water use and status. In the regions where the amount of precipitation and soil moisture will decrease, there is a high probability that g_n and E_n will decrease as well (Zeppel et al. 2014). When the contact between roots and soil solution remains adequate, then decreased E_n favours equilibration between Ψ_{pd} and Ψ_s (Ourcival and Berger 1995). However, under severe water deficit, when the contact weakens (Cochard et al. 1996), there will be an increasing probability for the development of PDD. At higher latitudes

where climate becomes more humid, higher soil water content and higher RH should favour higher g_n in plants (Zeppel et al. 2014; O’Keefe and Nippert 2018). As water saving is not very important in such conditions, it might happen that control over stomatal regulation becomes weaker. It has been demonstrated that leaves developed in high RH conditions close their stomata slower in stress conditions compared to leaves developed in moderate RH conditions (Fanourakis et al. 2011, 2016, 2020). In the first case, plants keep their stomata more open and transpire at higher rates also at night, which results in lower Ψ_{pd} and greater PDD compared to the latter case. In fact, Nejad and van Meeteren (2005) demonstrated on *Tradescantia virginiana* L. plants that the effect of high RH during leaf development was stronger on night-time stomatal responses (conductance, aperture and transpiration) compared to those in the daytime.

1.4. Aims of the thesis

The general objectives of the thesis are:

- To compare nocturnal stomatal conductance and PDD in temperate deciduous tree species differing in ecological demands and life strategies.
- To elucidate the environmental factors that govern nocturnal transpiration and water potential predawn disequilibrium (PDD) in northern broadleaved trees.
- To test whether increasing atmospheric humidity – a climate trend predicted for high latitudes – affects nocturnal water use in northern trees.

The following hypotheses were set:

1. Under ample soil water availability, fast-growing tree species are characterized by higher night-time stomatal conductance compared to slow-growing species, but this difference disappears under drought conditions.
2. High night-time atmospheric evaporative demand enhances PDD in deciduous trees under sufficient soil water supply.
3. During nights with dew formation, temperate broadleaved trees are able to harness foliar water uptake in case of soil water deficit.
4. Growing under elevated RH weakens nightly stomatal control, leading to larger nocturnal sap flux density and PDD in trees.

2. MATERIALS AND METHODS

2.1. Experimental set-up and species

All field experiments were conducted at the Free Air Humidity Manipulation (FAHM) site located at Rõka village (58°14' N, 27° 17' E), eastern Estonia. The study area belongs to the hemiboreal forest zone. The long-term average annual precipitation in the region is 650 mm, and the average air 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 Endogleyic Planosol (WRB) with an A-horizon thickness of 27 cm. Total nitrogen content in the A-horizon is 0.11–0.14%; C/N ratio is 11.4, and pH is 5.7–6.3. The study site was established on abandoned agricultural land in 2006–2007. It is a fenced area of 2.7 ha consisting of nine hexagonal experimental plots (Ø 14 m) planted with hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) and silver birch (*Betula pendula* Roth), which are surrounded by a hybrid aspen buffer zone. One-year-old micropropagated hybrid aspen plantlets were planted in the experimental area in the autumn of 2006. The stand density in the buffer zone is 2500 trees ha⁻¹ and in experimental plots, 10,000 trees ha⁻¹. In 2012, the trees were felled and the coppice shoots (stump and root sprouts) were allowed to emerge in hybrid aspen. Three sample plots were used as control plots (C), and three plots were humidified (H). Air relative humidity (RH) was increased in H plots using a misting technique to atomize/vaporize water, combined with a FACE-like technology to mix humidified air inside the plots. Humidification was applied in the daytime 6 days a week when ambient RH was <75% and mean wind speed <4 m s⁻¹.

Paper I

In 2013, the study was conducted on hybrid aspen coppice (mean height ± SE 1.40 ± 0.03 m) that had sprouted the same spring. Shoots were sampled from both C and H plots to find out if elevated daytime air humidity affects the development of PDD. In 2014, the study was carried out on 9-year-old hybrid aspen trees growing in the buffer zone of the FAHM site. Leaves from upper and lower thirds of the canopy were sampled to evaluate the effect of the length of the water transport pathway on PDD.

Paper II

In 2015, the study was conducted on 2-year-old hybrid aspen coppice shoots sampled from both C and H plots. Mean height (± SE) of the shoots was 3.25 ± 0.15 m, and mean diameter at 0.3 m height was 24.1 ± 1.2 mm at the end of the growing season. The relatively big size of coppice shoots was probably caused by the large root systems of the parent trees removed in 2012. Sapwood to leaf area ratio estimated by litterfall averaged $2.13 \times 10^{-4} \text{ m}^2 \text{ m}^{-2}$ prior to the beginning of leaf shedding.

Paper III

In 2017 and 2018, experiments were carried out in Percival AR-95 HIL (Percival Scientific Inc., USA) growth chambers. 48 micro-propagated hybrid aspen and 30 seed-grown silver birch saplings were planted into 10-L pots. A detailed description of the growing medium is given in the paper. The pots with saplings were weighed and watered every morning to restore the soil water reserve and to maintain the upper limit of the soil water content at 60% of the field capacity. From the weighting data, water consumption (g) of each plant was calculated. The night/day length in the chambers was 8/16 h. The night-time in growth chambers lasted from 9:00–17:00 and 8:30–16:30 h for hybrid aspen and silver birch, respectively. The daily photosynthetically active radiation (PAR) was kept at $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the top of the saplings. The sample trees were grown at two (hybrid aspen) or three (*B. pendula*) different air humidity regimes (high, moderate and low-RH treatment) at air temperature $\sim 21.6^\circ\text{C}$. The high-RH and low-RH treatments were characterised by the ~ 80 and 65% RH twenty-four hours a day, respectively. The moderate-RH treatment was characterised by the ~ 80 and 65% RH during night and day, respectively. In hybrid aspen, a jump of VPD was conducted in the middle of the night (Fig. 1A in **III**). The latter was not conducted on silver birch, as it was not applicable for low-RH treatment trees.

Paper IV

The experiment was conducted in a greenhouse of the Laboratory of Plant Ecology, Faculty of Bioscience Engineering, Ghent University, Belgium, in nine temperate tree species: 3- to 4-year-old *Alnus glutinosa* L. Gaertn., *Betula pendula*, *Fagus sylvatica* L., *Liquidambar styraciflua* L., *Quercus robur* L., *Robinia pseudo-acacia* L., *Sorbus aucuparia* L. and *Tilia cordata* Mill. (plant height 150–175 cm), and 2-year-old *Populus tremula* L. (plant height 125–150 cm) plants. The growth substrate was organic soil with organic matter content of 10% (Peltracom, Belgium), enriched with 4 g L^{-1} slow releasing fertiliser (Osmocote Standard 8–9 M, Osmocote Garden, USA). Ten seedlings per species were planted in 25-L pots (\varnothing 40 cm, height 25 cm) on 21 March 2018. Measurements were conducted from 9 May to 28 June 2018. Prior to measurements, five to eight of the healthiest trees per species were chosen for the study. After planting, all trees were regularly watered by drip irrigation every evening. On 29 May 2018, irrigation was stopped for half of the trees of all species in order to investigate the effect of drought on nocturnal water relations. The soil of these trees gradually dried out and the trees that showed visual signs of wilting ($\Psi_{\text{pd}} \leq -5 \dots -3 \text{ MPa}$) were removed from the experiment.

2.2. Recording of environmental factors

In all the studies, several environmental variables were continuously recorded in experimental sites. Air temperature (T_{A}) and RH were measured with HMP45A humidity and temperature probes (Vaisala, Finland) in the field studies (**I**, **II**) and

growth chamber study (III), and with SHT25 sensor (Sensirion, Switzerland) in the greenhouse experiment (IV). Soil water potential (Ψ_s) was measured with EQ2 equitensiometers (Delta-T Devices, UK) in field studies and with MPS-2 dielectric water potential sensors (Decagon Devices, USA) in the growth chambers. In the greenhouse, volumetric soil water content (SWC) was measured instead using a portable Theta Probe type ML2 (Delta-T Devices), and data was converted to Ψ_s by calibration with a tensiometer (CV5 U, Tensio-Technik, Germany) in a separate pot containing both sensors and filled with the same soil that was used for the experiment. In field studies, soil temperature (T_s) was also measured, using ST1 (Delta-T Devices) or 107-L soil temperature probes (Campbell Scientific, USA). Leaf wetness (LW) was monitored with LWS-1 dielectric surface wetness sensors installed next to the sample shoots and connected to Em50 data loggers (Decagon Devices). In field studies, the readings of T_A , RH, Ψ_s and T_s were stored as average values every 1–10 min with DL2e (Delta-T Devices) or CR1000 (Campbell Scientific) data loggers. In the greenhouse, the readings of T_A and RH were stored in custom-built loggers; the readings of SWC with a HH2 logger (Delta-T Devices). VPD was calculated according to Bolton (1980):

$$\text{VPD} = \left(1 - \frac{\text{RH}}{100}\right) \cdot 0.6112 \cdot \exp^{\frac{17.67 \cdot T}{T+243.5}}. \quad (1)$$

2.3. Water relations measurements

In all the studies, leaf water potential was measured with Scholander-type pressure chambers – custom-built (I, II) or industrially manufactured (PMS Instrument Company, USA; III, IV) instruments. Leaves were excised with a razor blade and inserted into a plastic bag with a wet tissue to prevent transpiration in the time between the excision and insertion into the pressure chamber. Ψ_{pd} was determined during 0.5 (I, II), 1 (III) or 1.5 hours (IV) prior to sunrise or before turning on the light in growth chambers (III). In 2013 and 2014 (I), Ψ_L was additionally measured 1 and 2 h after dawn to test whether the highest Ψ_L occurs always before dawn or could it happen later. In growth chambers, Ψ_L was additionally measured in the early- and middle-night, and daytime. In order to prevent night-time water losses and to estimate the contribution of nocturnal transpiration to PDD and the xylem water potential of branches (Ψ_B), we applied the bagged leaves technique (Brodribb and Holbrook 2003). Sample leaves were enclosed airtightly in Minigrip bags and covered with aluminum foil on the previous evening. In the field studies (I, II), three uncovered and two covered leaves per tree (2013 and 2015) or per canopy position (2014) were sampled to obtain Ψ_{pd} . In 2013 and 2014, the same was repeated also 1 and 2 h after the sunrise. In the greenhouse study (IV), Ψ_{pd} was determined immediately after measuring predawn stomatal conductance to water vapour (g_{pd}) on the same leaf. PDD between soil and leaf water potentials was calculated as a difference between Ψ_s and Ψ_{pd} .

In 2015 (II), sap flow was measured to estimate nocturnal water losses in hybrid aspen. We applied SFM1 sap flow meters (ICT International, Australia) based on the heat ratio method thoroughly described by Burgess et al. (2001). That method has the benefit of detecting low sap flow rates that are common during night-time. Because of the small diameter of the sample trees we installed only one sensor per tree just below the live crown. Twelve trees from four experimental plots were sampled simultaneously. To calculate the total water flux in the stem we measured stem diameter: two perpendicular measurements were taken above the sensors and two below the sensors approximately once a week. Bark thickness was subtracted from the average value of the four measurements to calculate the cross-sectional area of xylem. Sap flux density (F) was expressed on an hourly basis per unit leaf area ($\text{g m}^{-2} \text{h}^{-1}$). Zero flow was determined by constant readings at the end of the growing season after trees had shed all their leaves. Nocturnal sap flow (Q_n) was separated into nocturnal transpiration (E_n) and tissue refilling (R_n) using a forecasted model (Fisher et al. 2007; Alvarado-Barrientos et al. 2015; Yu et al. 2018). Refilling was interpolated using exponential decay function:

$$y = a \cdot b^t, \quad (2)$$

where t is time, and a and b are empirical constants. E_n was calculated as Q_n minus R_n (Fig. 1 in II).

In the growth chamber study (III), sap flow was recorded with a T4.2 sap flow systems (EMS Brno, Czech Republic). To express the sap flux density (F ; $\text{mmol m}^{-2} \text{s}^{-1}$), the tree foliage area was measured with a LI-3100C optical area meter (LI-COR Biosciences, USA). The daily tree water consumption, based on the weighing of the pots, was used to calibrate the sap flow data. The soil-to-leaf hydraulic conductance (K_{S-L} ; $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) was calculated from F and water potential difference between the soil and leaf ($\Delta\Psi$):

$$K_{S-L} = \frac{F}{\Delta\Psi}. \quad (3)$$

In the greenhouse study (IV), g_{pd} was measured (AP4 cycling porometer, Delta-T Devices) to estimate nocturnal stomatal openness. The measurements were started approximately 1.5 h before sunrise, sampling one leaf per tree. Also minimum leaf conductance (g_{min}) was determined, which was defined as the conductance through the cuticle and stomata at their maximum closure (Howard and Donovan 2010), induced by severe drought. Leaves of the drought-treated trees showing signs of wilting were used for this purpose before the entire tree was removed from the experiment.

2.4. Data analysis

The data from years 2013 and 2015 (**I**, **II**) collected from **H** and **C** plots was treated for most of the analysis as one dataset, since the effect of air humidification was statistically insignificant. In the 2014 study (**I**), Ψ and PDD data from different canopy layers were also pooled, as the mean values from the two layers were not significantly ($P > 0.05$) different from one another. In that study, the data points with negative PDD values that occurred at the end of the study period were removed from the analysis. In the greenhouse study (**IV**), on some occasions, when SWC exceeded field capacity (~60%) and water accumulated in a shallow vessel placed under the pot, the respective values of g_{pd} and PDD were excluded from the main data analysis.

Statistical analysis was conducted using Statistica 7 (StatSoft Inc., Tulsa, OK). The assumptions of normality 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. Relationships between the focal characteristics and independent continuous variables were analyzed by using simple linear, multiple linear or non-linear least squares regressions, and the effect of continuous variables was quantified by the coefficient of determination (R^2). The difference between the means of two groups was assessed with the Student's t -test. Analysis of variance (ANOVA) was applied to assess effects of categorical variables. The post hoc mean comparisons between the means of more than two groups were conducted using the Tukey's HSD test (**I**, **II**, **IV**). A repeated-measures and factorial ANOVA were applied to compare different treatment groups in the growth chamber study (**III**). Analysis of covariance (ANCOVA) was applied when the effect of both categorical and continuous factors on focal traits were assessed. The goodness of the models was expressed as R^2 . Type III or type IV (in case of unbalanced data sets) sums of squares were used in the calculations. Effect sizes of single variables were estimated as $SS_{\text{effect}}/(SS_{\text{effect}}+SS_{\text{error}})$ (**I**) or $SS_{\text{effect}}/SS_{\text{total}}$ (**II**, **IV**).

3. RESULTS AND DISCUSSION

3.1. Environmental variables governing nocturnal stomatal conductance and water use

In the greenhouse experiment (IV), predawn stomatal conductance (g_{pd}), used as an estimate of nocturnal stomatal conductance, differed significantly (ANCOVA, $P < 0.001$) between the nine temperate tree species involved in the experiment. Soil volumetric water content (SWC) was the only environmental factor that had an effect on g_{pd} , describing 22% ($P < 0.01$) of the variation in g_{pd} when all the species were pooled in one dataset. Nocturnal stomatal conductance increased with increasing SWC. When analysing all the species separately, then eight out of nine species demonstrated a significant positive relationship between SWC and g_{pd} (Fig. 1). This is an expected result – at night stomata of deciduous trees respond to soil water availability similarly as in the daytime. The same has been demonstrated for different species from various ecosystems and plant functional groups (Barbour and Buckley 2007; Howard and Donovan 2010; Ogle et al. 2012; Zeppel et al. 2012). However, the response of g_{pd} to SWC was in practice determined by species stomatal openness in moist soil conditions (g_{pd_wet} ; SWC = 40–60%; Fig. 5 in IV), but not by that in dry soil conditions (g_{pd_dry} ; SWC < 25%; $P = 0.68$). Thus, steeper slopes between SWC and g_{pd} in some species were caused by higher stomatal conductance under ample soil water content rather than by higher sensitivity to soil water deficit. g_{pd_wet} varied significantly ($P < 0.001$) among the species, ranging from 10.9 to 102.7 mmol m⁻² s⁻¹ (Table 2 in IV). Tree species was the only significant factor responsible for the variation in g_{pd_wet} . This result suggests that different species keep their stomata open at night to varying degrees when there is ample water in the soil. Bucci et al. (2016) proposed that night-time transpiration has probably a genetic basis. The highest mean g_{pd_wet} (102 mmol m⁻² s⁻¹) was observed in *P. tremula*. *A. glutinosa*, *B. pendula* and *F. sylvatica* demonstrated moderate values (30–50 mmol m⁻² s⁻¹), and the rest lower values of g_{pd_wet} (10–22 mmol m⁻² s⁻¹).

P. tremula demonstrated substantially higher nocturnal stomatal openness than all the other species ($P < 0.001$) sampled in the greenhouse experiment (IV). It is considered a characteristic of fast-growing shade intolerant pioneer and anisohydric tree species (Aasamaa and Söber 2001). Our finding is supported by high predawn soil-to-leaf hydraulic conductance (K_{S-L} ; Fig. 2B in III), necessary to provide adequate water supply to the leaves losing water through stomata kept open at night. *B. pendula* is also characterised as a fast-growing light-demanding tree species (Ellenberg 1988), but in contrast has isohydric stomatal behaviour (Uddling et al. 2004; Kupper et al. 2018). Similar nocturnal sap flux densities in *B. pendula* and hybrid aspen recorded in the growth chamber study (Figs. 1B and 3B in III) confirm that their stomata were open during the night. Species growing slower, like *Quercus robur*, *Tilia cordata*, *Sorbus aucuparia*, demonstrated quite low g_{pd_wet} (10–19 mmol m⁻² s⁻¹; Table 2 in IV). These results confirm my first

hypothesis, that fast-growing tree species keep their stomata more open at night in case of ample soil water availability, reducing stomatal constraints to gas exchange in the early morning and supporting, in this way, high growth rate.

L. styraciflua and *R. pseudoacacia* are also considered pioneer species (Ruiz-Sanchez and Ornelas 2014; Sitzia et al. 2016) but their stomatal behaviour differed from what we observed in *B. pendula* and *P. tremula*. These species originate from warmer southern regions, and they demonstrated quite low g_{pd_wet} . Our data suggests that the first hypothesis is valid for species from cooler and more humid regions. It has been proposed that fast-growing species may benefit from nocturnal or predawn stomatal opening through various mechanisms: enhanced nutrient transport to the leaves, enhanced O_2 delivery to parenchyma cells in the stem, removal of excess CO_2 or circadian priming of stomata for early morning photosynthesis (Caird et al. 2007; Dawson et al. 2007; Bucci et al. 2016). Resco de Dios et al. (2019) recently concluded from an extensive meta-analysis that the last mechanism – enhancement of photosynthesis in the early morning – is the most plausible one supporting higher growth rate of the respective species.

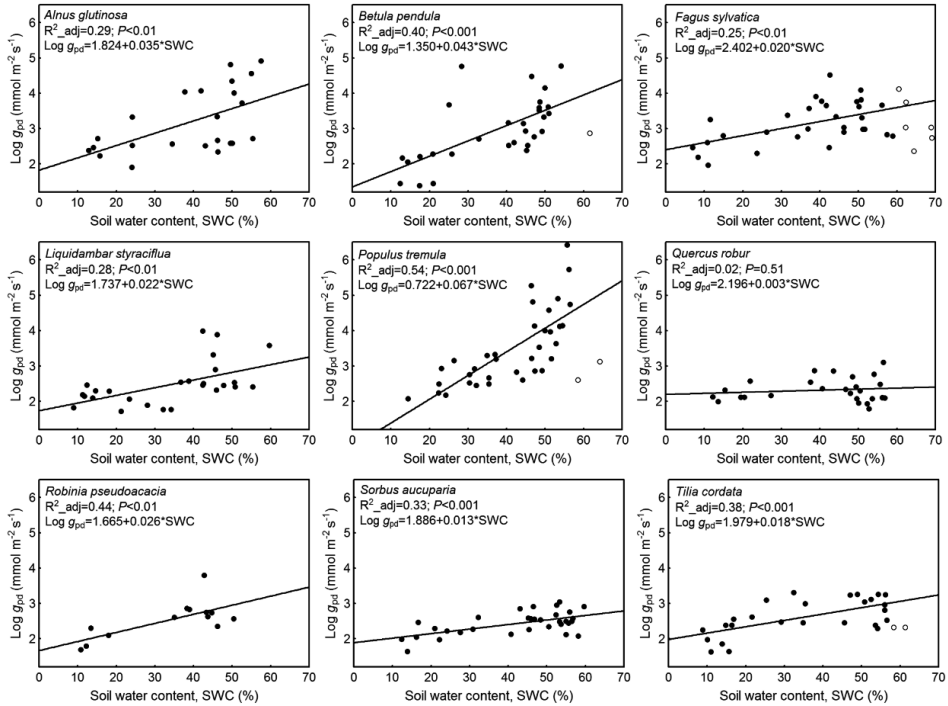


Figure 1. Relationships between soil volumetric water content (SWC) and natural logarithm of predawn stomatal conductance ($\text{Log } g_{pd}$) in seedlings of nine deciduous tree species. Open symbols denote the cases when SWC exceeded field capacity. The trendline is based on closed symbols.

Nocturnal stomatal behaviour of *Q. robur* differed from that of all other species – g_{pd} was insensitive to SWC ($P = 0.51$; Fig. 1). Moreover, mean g_{pd_wet} of *Q. robur* was very low ($10.9 \text{ mmol m}^{-2} \text{ s}^{-1}$) and did not significantly differ from g_{pd_dry} or from g_{pd} measured on wilted leaves, g_{min} (ANOVA, $P = 0.45$). In *S. aucuparia*, *R. pseudoacacia*, *L. styraciflua* and *T. cordata* g_{pd_wet} was also relatively low (Table 2 in IV), whereas in the first two species it did not differ from g_{pd_dry} ($P > 0.05$). Low nocturnal stomatal conductance ($4\text{--}16 \text{ mmol m}^{-2} \text{ s}^{-1}$) also appears to be characteristic of other *Quercus* species, but it differs significantly between drought-treated and well-watered trees (Cavender-Bares et al. 2007).

On the other hand, g_n is insensitive to SWC also in *Ulmus laevis* Pall., but it is relatively high both in well-watered and in drought-affected ($85\text{--}220$ and $75\text{--}225 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively) trees (Eller et al. 2017). Our results suggest that even in moist soil conditions some tree species keep stomata basically as closed as possible at night. There is no one single and universal explanation for this phenomenon. For example, *Q. robur*, *S. aucuparia* and *T. cordata* all are characterised by quite low growth rates (Ellenberg 1988). The same has been confirmed also for other tree species with relatively low growth rate (Daley and Phillips 2006; Marks and Lechowicz 2007; Howard and Donovan 2010). *L. styraciflua* and *R. pseudoacacia* are pioneer species, but compared to other studied species they originate from drier southern areas, where water deficiency is more common. That could be the reason why stricter stomatal control has evolved in these species, and the negative aspect of losing water during nights probably outweighs potentially positive consequences of nocturnal transpiration. *Q. robur*, *L. styraciflua* and *R. pseudoacacia* are also characterised as isohydric species (Aasamaa and Sõber 2001; Kjellgren et al. 2016; Moser et al. 2016), which refers to an overall conservative water-use strategy, including strict stomatal control during the night. One more trait is common for *Q. robur* and *R. pseudoacacia*: their highly conservative nocturnal water use is probably, at least partly, associated with the anatomical structure of their wood. They are ring-porous trees, whose xylem contains large vessels prone to embolism and only a few outer growth rings stay functional.

Several studies have compared nocturnal stomatal conductance of well-watered plants with that of drought-treated (Barbour and Buckley 2007; Ogle et al. 2012; Zeppel et al. 2012) or wilted plants (Howard and Donovan 2007; 2010), but we also compared the latter two with each other. In our greenhouse experiment, mean g_{min} ranged from 5.6 to $10.3 \text{ mmol m}^{-2} \text{ s}^{-1}$, but it did not significantly ($P > 0.05$) differ among the species. These values fall well within the range reported in the literature for other species (Caird et al. 2007; Howard and Donovan 2007; 2010). Mean g_{pd_dry} varied from 7.7 to $14.6 \text{ mmol m}^{-2} \text{ s}^{-1}$ and it did not also differ among the species involved ($P > 0.05$). In addition, g_{pd_dry} and g_{min} did not differ from each other in any of the species ($P > 0.05$). As we assume that g_{min} represents conductance of water vapour through the cuticle and stomata at maximum closure (Howard and Donovan 2007), the results indicate that under drought stress all of the studied species kept stomata tightly closed before sunrise. This kind of uniform response in all the species suggests that the trees that typically demonstrate

anisohydric behaviour during daytime do not necessarily follow the same pattern of behaviour during the night-time if they face soil water deficit. This means that species benefitting from nocturnal stomatal openness lose that advantage during drought. As drought episodes are predicted to become more frequent in Central and Southern Europe in the future, it might occur that the fast-growing trees will prove more susceptible to the climate change compared to slow-growing species.

In eight species out of nine involved in our greenhouse experiment, g_{pd} did not respond to VPD ($P > 0.05$), which ranged from 0.6 to 1.2 kPa. Only *T. cordata* demonstrated a significant positive trend ($R^2 = 0.61$; $P < 0.01$) with VPD. The data on the response of g_n to VPD variability reported in the literature are also controversial, but there are more reports about the negative effect of VPD on g_n (Ogle et al. 2012). Why should higher VPD enhance g_n in some cases is not still clear. Zeppel et al. (2012) suggest that VPD might affect stomatal regulation differently during night-time compared to daytime. The absence of VPD effect might be caused by too small range of nocturnal VPD in some studies, like in our experiment. The opposite was shown, for example, for *Ricinus communis* L., where g_n demonstrated negative response to VPD, while the latter ranged from 0.1 to 2.7 kPa (Barbour and Buckley 2007). However, as our analysis is based on predawn measurements, at a time when the stomatal responses are very likely under circadian control, i.e. late-night stomatal conductance is actively controlled (Resco de Dios et al. 2015), then small changes in VPD have only a slight effect on g_{pd} .

Although g_{pd} might not respond when changes in VPD are small, nocturnal sap flux density (F_n) and water use definitely depend on VPD. The field experiment on hybrid aspen (II) demonstrated that despite the fact that nocturnal VPD only ranged from 0 to 0.45 kPa, it had a strong positive influence on F_n ($R^2 = 0.82$; $P < 0.001$), whereas the stimulating effect was weaker in wet soil (Fig. 2). Our result confirms that even at low VPD, nocturnal water-use of broadleaved trees may be highly dependent on atmospheric conditions. As F_n represents both nocturnal refilling (R_n) and nocturnal transpiration (E_n), it is probable that E_n can respond to VPD even more sensitively than F_n reported here. The relationship between VPD and F_n was linear (Fig. 2), like it has been reported in other studies conducted in humid regions where nocturnal VPD remains low (Rosado et al. 2012; Kupper et al. 2018). These papers also confirm that g_n does not depend on changes in AED at low VPD values. Several studies conducted in drier regions report that the relationship between VPD and F_n becomes less steep at higher nocturnal VPD, compared to steeper VPD vs F_n slopes observed at low VPD values (Barbeta et al. 2012; Rosado et al. 2012; Alvarado-Barrientos et al. 2013; Resco de Dios et al. 2013). This suggests that even at night stomata react to high VPD with closing, to limit water losses.

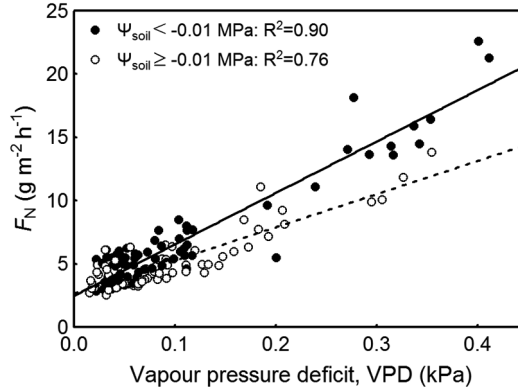


Figure 2. The relationship between vapour pressure deficit (VPD) and nocturnal sap flux density (F_n) in hybrid aspen coppice at different soil water statuses. Each data point represents a mean value of all trees ($n = 12$) in a single night.

3.2. Proportion of nocturnal water loss in daily total transpiration

The study on field-grown hybrid aspen (II) revealed that nocturnal sap flow (Q_n) constituted on average 7.0% of daily total sap flow, which equals daily total transpiration (E). However, Q_n consists of two components – nocturnal transpiration (E_n) and tissue refilling (R_n). E_n and R_n averaged 62% and 38% of Q_n , respectively, which means that E_n constituted 4.5% of the daily total transpiration (E_n/E). In many studies Q_n has been quantified, but only a relatively small number of them have separated Q_n into E_n and R_n . However, a strong positive relationship between VPD and nocturnal sap flow described hereinabove and observed in several studies (Sellin and Lubenets 2010; Gotsch et al. 2014; Zeppel et al. 2014) suggests that most of that sap flow is attributable to E_n . Compared to other studies (Fisher et al. 2007; Phillips et al. 2010; Alvarado-Barrientos et al. 2015; Yu et al. 2018) that have separated Q_n into the two components, E_n/E ratio in hybrid aspen is positioned at the lower end of the range (2.3–30%). That can be explained by cool and humid nights prevailing typically in Estonian forests during summers. However, in dry nights, E_n/E reached 14% in hybrid aspen. Mean E_n/E values exceeding 15% have been recorded in tropical montane cloud forest during the dry season (Alvarado-Barrientos et al. 2015). As regards congeneric species, Cirelli et al. (2016) demonstrated that E_n makes up 6–12% of total daily transpiration in different *Populus* species.

In our study on hybrid aspen, the contribution of E_n to Q_n (E_n/Q_n) was on average 62%, however, it varied in a wide range – 17–95%. Such high variability can primarily be explained by the variation of VPD during the previous day ($P < 0.001$). The latter determines to what extent trees' water stores deplete during a day, which in turn determines how large proportion of Q_n will be covered by R_n in the following night. Theoretically, the variation of E_n/Q_n should also be explained by the variation in nocturnal VPD: the higher the nocturnal VPD, the

bigger the contribution of E_n to Q_n (Phillips et al. 2010). However, our results do not support this conclusion. The average E_n/Q_n reported in other studies also differs a lot: it varies from 15% (Fisher et al. 2007) to 95% (Alvarado-Barrientos et al. 2015). This can be explained by two factors: (1) studies have been conducted in different ecosystems with various environmental conditions (incl. interactive effects on several ecological factors) and in diverse tree species; (2) different methods have been used to distinguish E_n from R_n in different studies. In arid and nutrient-deficient ecosystems, the percentage of both nocturnal transpiration and stomatal conductance significantly depends on soil nutrient availability (Bucci et al. 2016).

Our results suggest that on average 5% of the total daily water loss takes place during the dark period in hybrid aspen, which is a common tree species widely cultivated in northern countries. Considering also other studies and global climate trends leading to the rise in air temperature and AED, the absolute amount of water lost from the soil via nocturnal transpiration will rise. At an ecosystem level, that proportion is probably higher, as herbaceous plants also exhibit nocturnal transpiration (Costa et al. 2015; O’Keefe and Nippert 2018; Groh et al. 2019). Therefore, night-time transpiration should be taken into account in estimating stand and ecosystem water balance, and in making model-based predictions for future vegetation water use.

3.3. Environmental and intrinsic factors governing PDD

Predawn water potential disequilibrium (PDD) was observed in all the ten tree species tested in four studies (I, II and IV), while its magnitude depended on the experimental approach, being lower in field experiments. Mean PDD was small in the experiments conducted in hybrid aspen in 2013 and 2014 – 0.04 and 0.07 MPa, respectively, although single records after dry nights extended to 0.2–0.4 MPa (I); in 2015 it averaged 0.19 MPa (II). These values are within the range reported for *Picea abies* and *Vaccinium myrtillus* growing in the same region in the hemiboreal vegetation zone (Sellin 1999), and for tropical savanna trees sampled during the wet season (Bucci et al. 2005). In seedlings of nine temperate tree species grown in a greenhouse the mean PDD ranged from 0.24 to 0.67 MPa (IV). Higher PDD values recorded in the greenhouse experiment are similar with those reported for the savanna tree *Schefflera macrocarpa* (C & S.) Seem during dry season (Bucci et al. 2005), and for some desert shrubs and salt marsh perennials (Donovan et al. 2001). The relatively big difference in PDD values between the field experiments and greenhouse experiments is primarily attributable to VPD levels, which were significantly lower in natural conditions compared to the greenhouse ($P < 0.001$; 0–0.45 kPa versus 0.6–1.2 kPa, respectively). The effect of AED on the development of PDD is unequivocally proved by substantial differences in Ψ_{pd} between bagged and unbagged leaves. Freely transpiring uncovered leaves demonstrated significantly lower Ψ_{pd} values, leading to greater PDD (Fig. 2 in I). These findings seem to support the second hypothesis that higher atmospheric evaporative demand at night brings about larger PDD.

However, in my studies, PDD depended on VPD only in the field experiments with hybrid aspen (Fig. 3 and Table 3 in **II**), but not in any of the nine species in the greenhouse experiment (Table 3 in **IV**). On the one hand, the range of VPD (0.6–1.2 kPa) could be too small to induce significant variation in PDD in the greenhouse. But on the other hand, that raises a question why even smaller changes in VPD (0–0.45 kPa) in field conditions had an effect on PDD? Bucci et al. (2005) unequivocally demonstrated that the variation in PDD depends on VPD, however, VPD varied in a much wider range (0.3–3.5 kPa) in their study. Sellin (1999) showed that also in a conifer, PDD is still dependent on nocturnal AED under low VPD (0–0.6 kPa) conditions, which is in line with the current results on hybrid aspen.

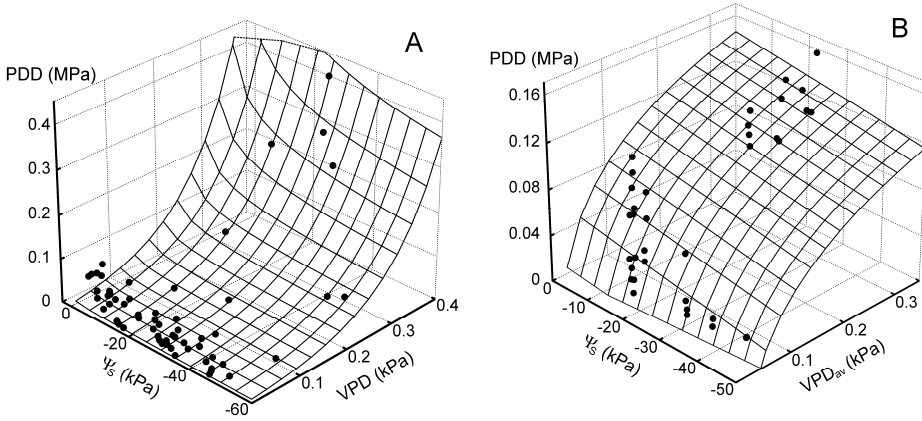


Figure 3. Predawn disequilibrium between soil and plant water potentials (PDD) in hybrid aspen as a function of atmospheric vapour pressure deficit (VPD) and soil water potential (Ψ_s). A) Coppice shoots, Ψ_s measured at a depth of 30 cm, VPD is a current vapour pressure deficit ($R^2 = 0.83$; $P < 0.001$). B) Young trees, Ψ_s measured at a depth of 40 cm, VPD_{av} is vapour pressure deficit averaged across 4 h prior to dawn ($R^2 = 0.71$; $P < 0.001$).

In field conditions (**II**), the major factor explaining the variation in PDD in 2-year-old hybrid aspen was soil-to-leaf hydraulic conductance (K_{S-L}), which explained 34.2% of the total variation ($P < 0.001$). PDD was inversely related to K_{S-L} . This result shows that lower plant hydraulic conductance, i.e. a less efficient hydraulic system, impedes water transfer to foliage and the achievement of equilibrium between leaf and soil water potentials by sunrise. In this study, K_{S-L} was also inversely related to Ψ_s ($P < 0.001$), which means that the hydraulic system conducted water less efficiently in trees exposed to wetter soil. That can likely be explained by overall moist soil conditions that prevailed throughout the whole study period in 2015. For some period, the soil was very wet ($\Psi_s > 0.01$ MPa), which was probably unfavourable for the trees because of possible hypoxic conditions that developed in the soil (Sellin et al. 2017). That conclusion is supported by lower F_n under very wet soil conditions compared to drier conditions (Fig. 2). Reduced hydraulic conductance due to temporary soil hypoxia might

also explain why mean PDD was significantly higher ($P < 0.001$) in 2015 compared to 2013 and 2014 studies. Hypoxia inhibits aquaporin gating, reduces root hydraulic conductivity and triggers stomatal closure (Kozlowski 1997; Kama-luddin and Zwiazek 2002; Tan et al. 2018). Reduced stomatal conductance in very wet conditions was demonstrated by some species in our greenhouse study (Fig. 1). In fact, the processes contributing to the inhibition of root hydraulic conductivity and root system conductance are complex and involve changes in both root morphology and the functions of aquaporins.

In greenhouse-grown trees, mean PDD was the greatest in *P. tremula* (0.67 MPa), differing significantly from that of all other species ($P < 0.001$). When analysing the whole dataset across all species, tree species, g_{pd_wet} , and night length combined described 54% of the total variation in PDD (Table 3 in IV). When analysing species separately, the results differed among the species. In *A. glutinosa*, PDD was almost entirely explained by g_{pd_wet} and night length ($R^2 = 0.94$; $P < 0.001$), in *B. pendula* and *P. tremula*, g_{pd_wet} was the only relevant independent factor ($R^2 = 0.50$; $P < 0.05$ and $R^2 = 0.34$; $P < 0.05$, respectively), but in *S. aucuparia*, night length was the only relevant independent factor ($R^2 = 0.34$; $P < 0.05$), and in the rest of the species none of the factors was statistically significant. The positive effect of g_{pd_wet} on PDD in *A. glutinosa*, *B. pendula* and *P. tremula* is an expected result as they were among the species with highest nocturnal stomatal openness. Our results confirm that nocturnal transpiration is one of the primary factors contributing to the development of PDD. The negative effect of night length in *A. glutinosa* and *S. aucuparia* shows that, in certain cases, nights may be too short for complete recharge of tree tissues with water, and therefore the equilibrium between Ψ_{pd} and Ψ_s cannot be achieved. The factors responsible for the variation in PDD in the other tree species still remain unclear. It is true that even small g_n allows some loss of water from the foliage. However, there are probably some other mechanisms for substantial discrepancy between Ψ_{pd} and Ψ_s present in tree species with very low g_{pd} .

Under certain conditions – in case of dry soil ($\Psi_s < -0.2$ MPa) and formation of dew on the leaves – Ψ_s proved lower than Ψ_{pd} , resulting in negative values of PDD in the droughty summer of 2014 (Fig. 1 in I). This indicates that leaves should have had an extra source of water. It is obvious that hybrid aspen leaves absorbed dew water formed during cool nights. The additional experiment a year later, where I submerged visually healthy leaves overnight suggests that hybrid aspen leaves indeed can absorb water through cuticle or microscopic damages. That approves the third hypothesis, confirming that northern trees growing in mesic sites can also absorb water from the leaf surface. Moreover, a Ψ_{pd} higher (i.e. less negative) than Ψ_s proves that nocturnal FWU not only affects predawn leaf water status and the magnitude of PDD, but can also reverse PDD (change from positive to negative). A study (Schreel et al. 2019) conducted in the framework of our greenhouse experiment at Ghent University on nine temperate tree species demonstrated that six out of nine and eight out of nine species were able to absorb water via their leaves in well-watered and drought conditions, respectively. Only *Q. robur* did not exhibit FWU in either treatment. Cavallaro et al. (2020) reported that all eight dominant plant species of the Patagonian steppe

tested in their study exhibited FWU. Foliar water uptake rates varied between 1.5 and 15% of the maximum transpiration rates across species. Taking into account the percentage of coverage of each species, cumulative FWU represented 1.6% of the total annual transpiration in this ecosystem. In recent years several studies have been conducted to shed light upon the phenomenon of FWU, which suggest that it is much more common and widely spread in diverse ecosystems than previously thought (Berry et al. 2019; Cavallaro et al. 2020; Schreel and Steppe 2020), and it can considerably affect leaf water status. The paradigm of water transfer in the soil-plant-atmosphere continuum is changing: water may enter the plant via different sites and move in two directions (e.g. reversed sap flow) depending on the water potential gradients.

The results of the field studies (I, II) suggest that under relatively moist (RH > ~90%) and cool ($T_A < \sim 15^\circ\text{C}$) atmospheric conditions during night-time, Ψ_{pd} (means ranging from -0.19 to -0.04 MPa) is a satisfactory estimate of Ψ_S . One should also consider the possibility that in very humid nights, the value of Ψ_{pd} might be altered by the formation of dew on leaf surfaces. Thus, using Ψ_{pd} as an accurate estimate of Ψ_S is constrained to nights with certain atmospheric conditions. In addition, it is necessary to test particular species for Ψ_{pd} , since our results demonstrated that broadleaved tree species differ largely in their nocturnal water relations and PDD (IV). High variation of PDD in the greenhouse experiment indicates that the Ψ_{pd} response is species-specific, being partly explained by differences in nocturnal stomatal openness between the species. More specifically, species keeping stomata more open during the night (e.g. *P. tremula*) lose more water, which leads to more negative Ψ_{pd} and its greater discrepancy from Ψ_S (Fig. 4). However, based on the results of the greenhouse experiment, one cannot conclude that Ψ_{pd} of the species keeping stomata basically closed (e.g. *Q. robur*, *S. aucuparia*) represents an adequate estimate of Ψ_S , because PDD remains moderately high in those species (Table 4 in IV and Fig. 4).

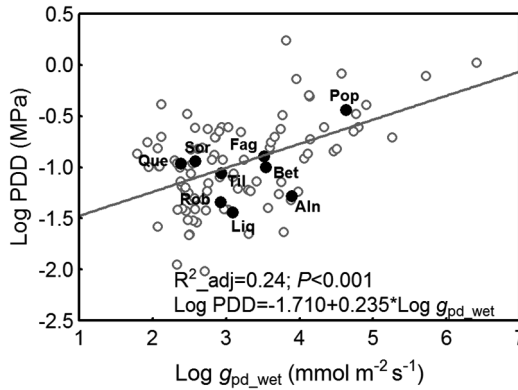


Figure 4. Relationship between predawn stomatal conductance (Log g_{pd}) and predawn water potential disequilibrium (Log PDD) in wet soil (SWC > 40%). The trendline is based on single measurements (grey open symbols). Solid black rings denote the average of each species: Aln – *Alnus glutinosa*, Bet – *Betula pendula*, Fag – *Fagus sylvatica*, Liq – *Liquidambar styraciflua*, Pop – *Populus tremula*, Que – *Quercus robur*, Rob – *Robinia pseudoacacia*, Sor – *Sorbus aucuparia*, Til – *Tilia cordata*.

3.4. Effect of elevated air humidity on nightly water use and PDD

The effect of artificially elevated air humidity on nocturnal plant water relations was investigated on hybrid aspen in field studies in 2013 (PDD, **I**) and 2015 (PDD and sap flow, **II**), and on hybrid aspen and silver birch in growth chambers (sap flow, **III**). In 2013, air humidification reduced daytime VPD by 5–10% (Niglas et al. 2015); in the rainy summer of 2015, humidification had no significant ($P > 0.05$) effect on mean daytime VPD. Our results indicate that elevating air humidity artificially through misting during daytime in field conditions affected neither nocturnal water use (**II**) nor development of predawn water potential equilibrium (**I**, **II**). However, F_n of hybrid aspen trees grown in a growth chamber under higher daytime RH (80%) responded positively to VPD increase at night (Fig. 1C in **III**), but not trees grown under moderate daytime RH (65%; Fig. 1D in **III**). That indicates that the stomata of the trees exposed to higher daytime RH did not respond or responded sluggishly to increased night-time evaporative demand compared to the trees exposed to moderate daytime RH. That might result from lower abscisic acid (ABA) concentration or reduced sensitivity to ABA in trees grown under high RH. It has been shown on *Lycopersicon esculentum* Mill. that plants grown under high RH had lower ABA concentration at night compared to moderate-RH conditions (Arve and Torre 2015). Therefore, too small and insignificant difference (**II**) in VPD between **H** and **C** plots does not allow us to state that increasing atmospheric humidity has no effect on trees' nocturnal water use at all. A study on hybrid aspen shoots cut from the FAHM site demonstrated that shoots grown in **H** plots exhibited higher predawn stomatal conductance compared to shoots from **C** plots when exposed to higher evaporative demand in a growth chamber (Rohula et al. 2017). Greater shifts in VPD and different species should be applied in future manipulative experiments. In a growth chamber experiment, saplings of *B. pendula* exposed to ~40% lower daytime VPD used significantly more water in the night-time (Kupper et al. 2017). These findings and study **III** demonstrate that in controlled conditions that create a greater difference in daytime VPD between manipulations, elevated RH may have an effect on plant nocturnal water relations, weakening stomatal control over water loss.

There could be several reasons why humidification had no effect on night-time water use of hybrid aspen in the field. First, the stump sprouts sampled in 2013 were too small and the effect of humidification might have been diminished by the high and lush herb layer. Second, the rainy summer in 2015 reduced the humidification effect – there were small but statistically non-significant ($P > 0.05$) differences in daytime VPD and RH between the humidity-treated and control plots. However, PDD in **H** plots was significantly larger compared to the control (Fig. 5). Third, exact measurement of small values of nocturnal water relations parameters (Ψ_{pd, g_n} , F_n) is complicated due to relatively big measurement errors, while morphological, anatomical (Kupper et al. 2011; Tullus et al. 2012; Jasińska et al. 2015; Sellin et al. 2015) and ecophysiological acclimations (Sellin

et al. 2013, 2017; Oksanen et al. 2019) induced by elevated air humidity may also flatten the responses of trees' water relations.

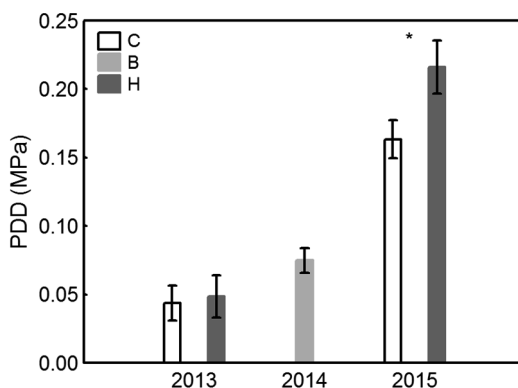


Figure 5. The magnitude of predawn water potential disequilibrium (PDD) in hybrid aspen coppice in humidified (H) and control (C) plots in 2013 and 2015, and in hybrid aspen saplings growing in buffer zone (B) in 2014. The significance of the difference between the treatments was estimated using the Students' *t*-test; * $P < 0.05$.

On a global scale, climate change endangers forests due to a decrease in precipitation, rising temperatures and heatwaves accompanied by forest fires and pest bursts, while at higher northern latitudes the climate rather will become more humid (IPCC 2013; Scoccimarro et al. 2015; EEA 2017). It has been suggested that, compared to conifers, broadleaved tree species can better acclimate to the conditions accompanying climate change, forcing boreal coniferous forests to retreat northward (Wang et al. 2013; Boisvert-Marsh et al. 2014; Linder et al. 2014). However, several studies conducted in the framework of the FAHM experiment have revealed that increasing air humidity has various effects on the morphology and functioning of deciduous tree species (Sellin et al. 2017; Oksanen et al. 2019). Reduced height, stem diameter and volume (Tullus et al. 2012), decreased carbon sequestration in trees, but increased sequestration in the understorey (Lõhmus et al. 2019), lower intrinsic water-use efficiency (Niglas et al. 2014), decreased transpirational water flux and concomitant diminished nutrient supply to the foliage (Sellin et al. 2013) are only some of many alterations evoked by increased air humidity in hybrid aspen and silver birch. Thus, the advantages of deciduous tree species over conifers might not be realized in the context of climate change, when warming is accompanied by increasing air humidity and soil moisture.

4. CONCLUSIONS

This thesis aimed to elucidate nocturnal and predawn water relations of temperate deciduous tree species and the possible effect of elevated air humidity on them. The following conclusions can be drawn based on the results obtained:

1. Under ample soil water availability, fast-growing pioneer tree species (e.g. *Populus tremula*, *Betula pendula*, *Alnus glutinosa*) exhibit relatively high night-time stomatal conductance (g_n) compared to slow-growing late successional species (e.g. *Quercus robur* and *Tilia cordata*). The exceptionally low g_n observed in pioneer species *Liquidambar styraciflua* and *Robinia pseudo-acacia* is probably attributable to their origin from warmer southern regions of the temperate zone, where, growing in drought-prone habitats, they have evolved a for more conservative stomatal behaviour. Northern tree species originating from cool and more humid environments probably benefit from higher g_n , reducing stomatal constraints and supporting high photosynthetic rates in the early morning, which is typical to pioneer species. Under drought conditions the differences between the species diminished, resulting in low g_n in all species. Most likely the harm from keeping stomata open during night under drought conditions is greater than its potential positive effect.
2. Due to incomplete stomatal closure, high night-time atmospheric evaporative demand brings about water losses from the foliage of deciduous trees at night, which leads to considerable predawn water potential disequilibrium (PDD) between soil and leaves. Tree species differing in ecological demands and life strategies differ in the magnitude of PDD under identical environmental conditions. Even in natural conditions of the hemiboreal vegetation zone, PDD can develop in trees after drier and warmer summer nights, suggesting that predawn leaf water potential (Ψ_{pd}) is not a reliable estimate of soil water potential (Ψ_s).
3. Our experiments proved that hybrid aspen trees are able to absorb water from the leaf surface, exhibiting foliar water uptake. Less negative Ψ_{pd} compared to Ψ_s in several nights coincided with the occurrence of dew in a drought period, when water film formed on leaf surfaces. Dew formation and foliar water uptake are additional factors that might bias Ψ_{pd} and undermine its usage as a proxy of Ψ_s .
4. In the growth chamber experiment, hybrid aspen saplings grown under elevated air humidity responded with increased sap flux density to a rise in atmospheric evaporative demand at night, which is evidence of weakened stomatal control over water loss. Although the field studies did not support that finding, this point should be addressed in further studies. Taking into account the regional climate trends, it is very likely that the proportion of nocturnal water losses in total daily transpiration of trees as well as the necessity for considering nocturnal transpiration in calculations of landscape or ecosystem water balance will increase in the future.

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SUMMARY IN ESTONIAN

Õine veevahetus ja koidueelne veepotentsiaalide tasakaalustumatus parasvöötme heitlehistel puuliikidel

Taimelehtede epidermis paiknevad väiksed poorid – õhulõhed, mille kaudu CO₂ difundeerub taime sisemusse ja taimest väljub veeaur – toimub transpiratsioon. Taimed on võimelised sõltuvalt keskkonnatingimustest õhulõhede avatust reguleerima, et kontrollida veekadusid lehest. Traditsiooniline käsitlus eeldab, et öösel, kui fotosüntees ei ole valguse puudumise tõttu võimalik, hoiavad taimed õhulõhed suletuna. Praeguseks on siiski teada, et paljud liigid hoiavad neid ka öösel avatuna. Õist õhulõhede avatust võivad mõjutada mitmed keskkonnategurid: mulla niiskus, suhteline õhuniiskus, õhu temperatuur, tuul, toitainete sisaldus mullas. Öisest õhulõhede avatusest tingituna kaotavad puud ka öösel vett, mis moodustab keskmiselt 10–15% kogu ööpäevasest transpiratsioonist. Sõltuvalt geograafilisest regioonist, kasvukoha eripärast ja liigi omadustest võib see number oluliselt varieeruda.

Õine veekadu võib põhjustada võrreldes olukorraga, kui õhulõhed oleksid öösel täielikult suletud, koidueelsel ajal lehtede madalama veestaatuse, kui seda võimaldaks mullavee kättesaadavus. Taimede veestaatuse mõõduna kasutatakse kõige sagedamini veepotentsiaali (Ψ), mis väljendab mingis keskkonnas, organismis, koes vm. oleva vee potentsiaalset energiat (tavaliselt negatiivse väärtusega) puhta vee suhtes normaaltingimustes (selle väärtus on null). Lehe koidueelset veepotentsiaali (Ψ_{pd}) kasutatakse ökofüsioloogilistes uuringutes tihtipeale mulla veestaatuse hinnanguna, kuna taime veestaatus peaks päikesetõusuueelseks ajaks tasakaalustuma mulla omaga. Kuid öiste veekadude tagajärjel ei pruugi Ψ_{pd} mulla veepotentsiaaliga tasakaaluseisundit saavutada, mistõttu esineb nähtus, mida kutsutakse koidueelseks veepotentsiaalide tasakaalustumatuseks (ingl. k. *predawn disequilibrium*, PDD). Sellises olukorras ei kanna Ψ_{pd} väärtus enam adekvaatset hinnangut mulla veestaatuse kohta. Lisaks öisele õhulõhede avatusele võivad PDD-d mõjutada muudki faktorid, mida käesolevas töös uuriti.

Praegused kliimamudelid ennustavad troposfääri alumistes kihtides temperatuuri tõusu üle kogu maakera. Enamikes piirkondades madalatel ja keskmistel laiuskraadidel kaasneb sellega sademete vähenemine ning pöudade ja kuuma-lainete sagenemine. Kuid põhjapoolkera kõrgematel laiuskraadidel, s.h. Põhja-Euroopas, kus asub ka Eesti, ennustatakse sademete hulga suurenemist ja sagene-mist. Sagenevad vihmahood suurendavad lokaalsel või regionaalsel tasandil ka suhtelist õhuniiskust, eriti metsaökosüsteemides, kus suur osa vihmaveest seotakse puude võrastikus. Suurenenud õhuniiskusel võib olla taimedele suurem mõju vegetatsiooniperioodi alguses, kui toimub lehtede areng. Senised Metsa-ökosüsteemi õhuniiskusega manipuleerimise eksperimendi (FAHM) tulemused näitavad, et suurenenud õhuniiskusel on oluline mõju lehtpuude kasvule ja mitmetele füsioloogilistele näitajatele (vähenenud toitainete omastamine mullast,

vähenenud fotosünteesivõime, häiritud lämmastiku metabolism, tärglase akumuleerumine lehtedes jm.). Seni pole aga teada, kas suureneval õhuniiskusel on mõju ka öisele õhulõhede regulatsioonile ja taimede koidueelsele veestaatusele.

Töö üldisemateks eesmärkideks olid:

- Võrrelda öist/koidueelset õhulõhede juhtivust (g_s) ja PDD-d parasvöötme heitlehistel puuliikidel, mis erinevad ökoloogiliste nõudluste ja elustrateegiatega poolest.
- Selgitada välja, millised keskkonnafaktorid mõjutavad looduslikes tingimustes puude öist/koidueelset õhulõhede juhtivust ja transpiratsiooni ning PDD-d.
- Selgitada välja, kas kasvamine suurenenud suhtelise õhuniiskusega keskkonnas mõjutab puude öist veekasutust ja PDD esinemist.

Doktoritöö aluseks olevad katsed viidi läbi hübriidhaaval (*Populus tremula* L. × *P. tremuloides* Michx.) välitingimustes Rõka külas asuval FAHMi katsealal, üheksa parasvöötme lehtpuuliigi seemikutel Genti Ülikooli (Belgia) kasvahoones ning hübriidhaaval ja arukasel (*Betula pendula* Roth.) TÜ ökofüsioloogia õppetooli kasvukambrites.

Keskmine koidueelne g_s varieerus uuritud liikide vahel laiades piirides ($10.9\text{--}102.7\text{ mmol m}^{-2}\text{ s}^{-1}$), kui muld oli mõõdukalt niiske (mullaveesisaldus, $\text{SWC} > 40\%$). Kõrgem õhulõhede juhtivus registreeriti kiirema kasvuga liikidel, millest omakorda eristus kõrgeima keskmise koidueelse g_s -ga harilik haab (*Populus tremula* L.). Aeglasema kasvuga liigid nagu harilik tamm (*Quercus robur* L.) ja harilik pärn (*Tilia cordata* Mill.) demonstreerisid võrdlemisi madalat õhulõhede avatust. Saadud tulemus viitab sellele, et öine/koidueelne õhulõhede avatus annab osadele liikidele teatud eelise, mis soodustab puude kiiremat kasvu. Selle seose kõige tõenäolisemaks seletuseks on varahommikune kõrge fotosünteesi intensiivsus neil liikidel, mis oma õhulõhed aegsasti enne koitu avavad, vältimaks piiranguid gaasivahetusele. Kuid on näidatud, et öine transpiratsioon soodustab ka toitainete efektiivsemat omastamist mullast, toetades sellega produktsiooni.

Koidueelne g_s korreleerus positiivselt mulla veesisaldusega kaheksal puuliigil üheksast. Vaid tamm hoidis öösi õhulõhed ühtlaselt suletuna nii kuiva kui märja mulla tingimustes. Samas kuiva mulla ($\text{SWC} < 25\%$) korral hoidsid kõik liigid oma õhulõhed praktiliselt suletuna. Sellest võib järeldada, et osa liike reageerib mulla niiskuse muutustele sarnaselt nii päeval kui öösel – põua tingimustes õhulõhede juhtivus väheneb, õhulõhed sulguvad. Teiselt poolt liigid, mis ka põua tingimustes hoiavad päeval ajal õhulõhed suhteliselt avatuna (anisohüdrilised liigid), sellist suundumust koidueelsel ajal ei demonstreerinud, vaid vähendasid samuti õhulõhede juhtivust. Seega erineva veekasutusstrateegiaga liikide õhulõhed käituvad põua tingimustes pimedal ajal väga sarnaselt.

Hübriidhaava öise ksüleemivoolu – s.o. veevoog mööda juhtkudesid juurtest lehtedesse – andmetest arvatud öine transpiratsioon moodustas keskmiselt 4.5% kogu ööpäevasest transpiratsioonist. Öine ksüleemivool korreleerus positiivselt atmosfääri veeaururõhu defitsiidiga (VPD), olgugi et viimane varieerub

hemiboreaalses võõndis öösiti metsas võrdlemisi vähe. Kõrgema VPD korral, s.t. kuivematel ja soojematel öödel oli ksüleemivoolu intensiivsus keskmisest kuni kuus korda kõrgem. Saadud tulemused kinnitavad ühemõtteliselt, et hübriidhaava õhulõhed pidid olema öösel vähemalt osaliselt avatud ning et õine veevoog läbi puu sõltub oluliselt atmosfääri tingimustest.

Nii kasvuhoones kui välitingimustes korraldatud eksperimentides leidis kinnitust PDD esinemine parasvöötme puudel. PDD suurus oli oluliselt väiksem välikatsetes (0.04–0.19 MPa) võrreldes kasvuhoone katsega (0.24–0.67 MPa). Selle üheks põhjuseks võib kindlasti pidada kõrgemat VPD-d kasvuhoones, mis toetas kõrgemat õist transpiratsiooni ja mis omakorda tingis madalama Ψ_{pd} . Eestis läbi viidud välikatsete käigus olid ööd pigem jahedad ja niisked, mistõttu enamikel öödel esines kaste, mis takistas vee aurumist lehtedest ning Ψ_{pd} oli lähedal tasakaaluseisundile mullaga, s.t. PDD oli nullilähedane. Avatud õhulõhede olulisust PDD kujunemise juures kinnitab kasvuhoone katses kõige suurema PDD esinemine h. haaval, mille koidueelne õhulõhede juhtivus oli liikidest kõrgeim. Osadel liikidel sõltus PDD ka öö pikkusest – mida lühem oli öö, seda suurem oli PDD. See tulemus näitab, et mõne liigi jaoks ei ole ööd alati piisavalt pikad, et puu kõik osad (tüvi, oksad, lehed) jõuaksid öö jooksul veega uuesti täituda, mistõttu ei tasakaalustu lehtede veepotentsiaal koidueelseks ajaks mulla omaga. See võib olla seotud nende liikide anatoomiliste iseärasustega, mis ei lase mullast omastataval veel piisavalt kiiresti kõikidesse taimeosadesse jõuda.

Teatud keskkonnatingimustes – kuiv muld koos kaste esinemisega öösel – tuli ette olukordi, kus hübriidhaava lehtede Ψ_{pd} oli vähem negatiivne kui mulla veepotentsiaal, mis tähendab seda, et lehtede veestaatus olid kõrgem kui mullal. See viitab asjaolule, et lehed pidid kusagilt mujalt kui mullast lisavett saama, milleks oligi kastevesi. Täiendavalt läbi viidud katse, mille käigus visuaalselt tervete lehtede labad ööks vette sukeldati, kinnitas, et hübriidhaab on võimeline lehtede pinnalt vett absorbeerima. See aga lisab täiendava tingimuse Ψ_{pd} kasutamisele mulla veestaatuse hinnanguna – jahedatel ja kastestel öödel, kuid kui mullas valitseb veedefitsiit, ei pruugi Ψ_{pd} mulla seisundit adekvaatselt peegeldada.

Kasvukambris korraldatud eksperiment näitas, et kõrgema päevase õhuniiskuse tingimustes kasvanud hübriidhaabade ksüleemivool tegi märgatava tõusu öösel, kui õhuniiskust järsult vähendati. Mõõduka õhuniiskuse tingimustes kasvanud puude puhul sellist tõusu ei täheldatud. Ksüleemivoolu tõus esimesel juhul viitab sellele, et kõrgema õhuniiskuse käes kasvanud puud ei vähendanud õhulõhede avatust või tegid seda väiksemal määral, mis näitab nende õhulõhede tundlikkuse vähenemist õhuniiskuse muutuste suhtes. Välikatsed FAHM katsealal ei kinnitanud suurendatud õhuniiskuse mõju hübriidhaava õisele ksüleemivoolule ega PDD kujunemisele. Sellisel tulemuste lahknevusel võib olla erinevaid seletusi. Ühelt poolt olid suved, mil välikatsed toimusid, keskmisest sajusemad, mis niisutustöötuse mõju välitingimustes kahandas. Lisaks olid eksperimendi esimesel aastal puud veel väiksed, nii et lopsakas alustaimestik võis samuti niisutuse mõju vähendada. Teisest küljest ei pruugi ksüleemivool ega ka Ψ_{pd} olla piisavalt tundlikud karakteristikud, eriti arvestades õhuniisutusest indutseeritud puude

morfoloogilist, anatoomilist ja füsioloogilist kohanemist. Seda eriti jahedatel põhjamaistel öödel, mil atmosfääri evaporaatiivne nõudlus on väga madal.

Doktoritööst selgus:

- Parasvöötme lehtpuuliikide koidueelne õhulõhede juhtivus varieerub piisava mulla veevarustuse tingimustes liigiti märkimisväärselt, olles kiirekasvulistel puudel kõrgem kui aeglase kasvuga liikidel. Põua tingimustes see erinevus kaob.
- Hübriidhaaval sõltub õine ksüleemivool atmosfääri nõudluse tasemest, mis viitab samuti õisele õhulõhede avatusele ja sellega kaasnevale transpiratsioonile. Umbes 5% kogu ööpäevasest transpiratsioonist toimus öösel.
- Nii välikatsetes uuritud hübriidhaaval kui ka üheksal kasvuhoones testitud lehtpuuliigil esineb koidueelne veepotentsiaalide tasakaalustumatus, mille suurus sõltub positiivselt VPD-st ja õhulõhede juhtivusest. Mida enam on õhulõhed avatud ja kõrgem on atmosfääri nõudlus, seda suurem on PDD, mistõttu tuleks teatud tingimustes olla ettevatlik Ψ_{pd} kasutamisel mulla veestaatuse hinnanguna.
- Hübriidhaab on võimeline öösel lehe pinnalt kastevett omastama, mistõttu tuleb arvestada selle võimaliku mõjuga Ψ_{pd} ja PDD kujunemisele niiskete ja jahedate ööde järgselt.
- Kõrgenenud päeval suhtelisel õhuniiskusel on mõju lehtpuude õisele õhulõhede regulatsioonile – stomataarne kontroll veekadude üle nõrgeneb, kuid seda on keeruline tuvastada välikatse tingimustes. Võttes arvesse regionaalseid kliimatrende, on väga tõenäoline, et tulevikus suureneb õiste veekadude osakaal puude ööpäevasest transpiratsioonis ning ka vajadus arvestada õise transpiratsiooniga maastike või ökosüsteemide veebilansi koostamisel.

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