

GRISTIN ROHULA-OKUNEV

Effects of endogenous and
environmental factors on night-time
water flux in deciduous woody tree species



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GRISTIN ROHULA-OKUNEV

Effects of endogenous and
environmental factors on night-time
water flux in deciduous woody 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** Kupper P, **Rohula G**, Saksing L, Sellin A, Lõhmus K, Ostonen I, Helmi-saari HS, Sõber A. 2012. Does soil nutrient availability influence night-time water flux of aspen saplings? *Environmental and Experimental Botany* **82**: 37–42.
- II** **Rohula G**, Kupper P, Räim O, Sellin A, Sõber A. 2014. Patterns of night-time water use are interrelated with leaf nitrogen concentration in shoots of 16 deciduous woody species. *Environmental and Experimental Botany* **99**: 180–188.
- III** **Rohula G**, Tulva I, Tullus A, Sõber A, Kupper P. 2017. Endogenous regulation of night-time water relations in hybrid aspen grown at ambient and elevated air humidity. *Regional Environmental Change* **17**: 2169–2178.
- IV** Kupper P, **Rohula G**, Inno L, Ostonen I, Sellin A, Sõber A. 2017. Impact of high daytime air humidity on nutrient uptake and night-time water flux in silver birch, a boreal forest tree species. *Regional Environmental Change* **17**: 2149–2157.
- V** Kupper P, Ivanova H, Sõber A, **Rohula-Okunev G**, Sellin A. 2018. Night and daytime water relations in five fast-growing tree species: Effects of environmental and endogenous variables. *Ecohydrology*
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The participation of the author in preparing the listed publications is as follows:

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

LIST OF ABBREVIATIONS

A_L	total leaf area (cm^2)
E	transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$)
E_{ap}	shoot artificial predawn transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$)
E_n	shoot night-time transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$)
FAHM	Free Air Humidity Manipulation experiment
F	sap flux density ($\text{mmol m}^{-2} \text{s}^{-1}$)
F_d	daytime sap flux density ($\text{mmol m}^{-2} \text{s}^{-1}$)
F_n	night-time sap flux density ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_{ap}	artificial predawn leaf conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_c	whole-tree canopy conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_d	daytime leaf conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_{n1}	'early night' leaf conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
g_{n5} or g_{pd}	'predawn' leaf conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
INT	increase in shoot night-time transpiration rate at artificial predawn (%)
K	shoot hydraulic conductance ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
N	nitrogen
[N]	nitrogen concentration of leaves (%)
NWU	night-time water use percentage from daytime water use (%)
P	phosphorus
[P]	phosphorus concentration of leaves (%)
P	atmospheric pressure (kPa)
PAR	photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
P_n	net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
R_d	dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
R_1	'early night' dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
R_5	'predawn' dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
RH	air relative humidity (%)
T_A	air temperature ($^{\circ}\text{C}$)
VPD_L	vapour pressure difference between leaf and atmosphere (kPa)
VPD	air vapour pressure deficit (kPa)
Ψ_L	leaf water potential (MPa)
$\Delta\Psi$	water potential gradient (MPa)

I. INTRODUCTION

1.1 The night-time transpiration phenomenon

Different species from a diverse range of genera and life forms and in all biomes may lose a substantial amount of water at night due to incompletely closed stomata (Benyon 1999; Snyder et al., 2003; Scholz et al., 2007; Caird et al., 2007; Forster 2014). Night-time transpiration rates are typically 5 to 30% of those during the day (Snyder et al., 2003; Caird et al., 2007; Phillips et al., 2010; Forster, 2014; Konarska et al., 2016), whereas the highest rates of night-time conductance and water loss (up to 25% of daytime water loss or more) are observed in species growing in deserts (Ogle et al., 2012), savannahs (Rosado et al., 2012) and Mediterranean ecosystems (Barbeta et al., 2012). Night-time transpiration is lower during the winter than in other temperate seasons, and significantly lower in the wet season than in the dry season (Forster, 2014). Nevertheless, variations in night-time transpiration do not simply owe to environmental differences but also to intra- and inter-specific physiological traits (Daley and Phillips, 2006; Phillips et al., 2010; Zeppel et al., 2010; Rosado et al., 2012). Night-time water fluxes constitute a significant factor in the annual water budget of forested ecosystems, and therefore have a substantial impact on global evapotranspiration at ecosystem scales (Resco de Dios et al., 2015).

1.2 Effects of endogenous factors on the regulation of night-time water flux

Numerous recent studies have demonstrated that night-time stomatal conductance is not stable throughout the night. An endogenous, gradual increase in the stomatal opening before dawn has been described in various species from different environments (Caird et al., 2007; Howard and Donovan, 2007; Resco de Dios et al., 2012, 2013), whereas the temporal pattern of night-time stomatal conductance is regulated by the circadian clock. Circadian clocks are ubiquitous in nature and are present in almost all groups of organisms, including plants (Bell-Pedersen et al., 2005). The circadian clock as an endogenous timer of plant metabolism controls the temporal pattern of transcription in photosynthesis, stomatal opening, and other physiological processes (Hubbard et al., 2015; Resco de Dios et al., 2016; Garcia-Plazaola et al., 2017). Furthermore, Gessler et al. (2017) found that night-time dark respiration at the leaf-level operates under circadian control. They demonstrated that circadian regulation as an adaptive memory to adjust plant metabolism is based on the environmental conditions of previous days. Similarly, Resco de Dios et al. (2012) identified a strong correlation between the daily pattern of light and temperature with endogenous rhythms, obscuring the potential importance of endogenous controls. It is possible that daily net ecosystem exchange may be controlled by a combination

of endogenous and exogenous factors (Doughty et al., 2006; Resco de Dios et al., 2012).

It is known that starch metabolism may directly affect endogenous stomatal opening by providing an osmoticant for endogenous stomatal regulation, whereas the lack of osmoticants results in the exclusion of pre-dawn stomatal opening in leaves with low starch content (Easlon and Richards, 2009). Lasceve et al. (1997) demonstrated that starch-deficient *Arabidopsis thaliana* L. Heynh. mutant plants had no endogenous stomatal opening in darkness, suggesting that starch metabolism is involved in the regulation of night-time stomatal conductance. Guo et al. (2003) showed that an *Arabidopsis* guard cell nitrate transporter mutant has reduced stomatal opening in response to low CO₂ in the dark. Thus, the products of starch metabolism are not alone in potentially forming osmoticant for the endogenous pre-dawn stomatal opening. Several osmoticums are involved in stomatal regulation at night, including soluble sugars and nitrate ions (Guo et al., 2003; Easlon and Richards, 2009; Zhao et al., 2016; Müller et al., 2017; Gessler et al., 2017).

The predawn stomatal opening may facilitate photosynthetic carbon fixation during early daylight hours by reducing diffusional limitations to CO₂ uptake at dawn (Oren et al., 2001; Daley and Phillips, 2006; Dawson et al., 2007). Resco de Dios et al. (2016) found that genotypic variation in *Eucalyptus camaldulensis* Dehnh. in predawn stomatal conductance was closely related to early morning stomatal conductance and plant carbon assimilation. They suggested that strong circadian regulation promotes higher daytime carbon assimilation and plant growth. Similarly, Dodd et al. (2005) showed that *Arabidopsis* plants with internal clocks in resonance with day-night cycles can fix more carbon, grow faster and survive better than mutants with impaired rhythmicity. However, Auchincloss et al. (2014) did not find any evidence that predawn stomatal opening could enhance early-morning photosynthesis in well-watered *Helianthus Annuus* L. plants. Nevertheless, predawn stomatal conductance might represent an adaptive response in water-limited ecosystems, resulting in a rapid stomatal response to early morning light, coincident with a lower vapour pressure deficit (Resco de Dios et al., 2016). This strategy would potentially maximise carbon assimilation in daylight. Circadian regulation is the most plausible explanation for the morning increase in CO₂ uptake and the afternoon decline in CO₂ uptake (Resco de Dios et al., 2012).

1.3 Interactions between mineral nutrient acquisition and night-time water flux

Night-time stomatal opening appears to represent significant, widespread behaviour in plants. It may at first seem to be a wasteful process because it leads to water loss at night, a time when carbon fixation is not possible. Nevertheless, night-time transpiration is considered impactful to overall plant function and

may outweigh the cost of nocturnal water loss. One potential benefit of night-time transpiration is increased nutrient uptake (Snyder et al., 2003). Previous studies have shown that N availability partially regulates transpiration (Cernusak et al., 2007; Garrish et al., 2010; Matimati et al., 2014), whereas plants can respond to nutrient limitation by varying their transpiration-driven mass-flow of nutrients (Cramer et al., 2008). Furthermore, it has been proposed that night-time stomatal opening may constitute an adaptive response in nutrient-poor conditions by increasing nutrient uptake or nutrient transport to distal parts of the plant via transpiration-induced mass-flow (Snyder et al., 2003; Ludwig et al., 2006). However, Howard and Donovan (2010) demonstrated in *Populus* species that although night-time water loss was under stomatal control, it was not regulated by soil nitrogen availability. Their findings did not support the notion that high nocturnal transpiration rates are linked to greater N uptake. In their study, soil nutrients only affected night-time stomatal conductance through secondary water stress. Thus, night-time transpiration is highly sensitive to water stress, but may not directly respond to soil nitrogen availability (Howard and Donovan, 2007, 2010; Christman et al., 2009). In contrast, Eller et al. (2017) found that under conditions of N-deficiency, well-watered *Fraxinus excelsior* L. trees demonstrated higher night-time stomatal conductance. They showed that the responses of night-time stomatal conductance in nutrient acquisition is contingent on the species and its nutrient uptake strategy. Previous studies have shown that night-time transpiration is typical of shade-intolerant species that have relatively high overall growth rates and leaf nitrogen concentrations (Daley and Phillips, 2006; Marks and Lechowicz, 2007). However, night-time water flux may also enhance nutrient transport within trees by providing oxygen to sapwood parenchyma cells that function in nutrient transport and storage (Daley and Phillips, 2006; Wittmann and Pfanz, 2014). Therefore, night-time transpiration may play a role of some functional importance in enhancing plant growth and fitness, and the potential gains of night-time transpiration are likely to be most significant amongst fast-growing tree species (Marks and Lechowicz, 2007). Nevertheless, night-time water flux may play a role in nutrient acquisition, although more studies on various species in controlled environmental conditions are needed to elucidate the possible effect of stomatal conductance in nutrient uptake at night.

1.4 Effects of air humidity on night-time stomatal conductance and water flux

It has long been known that stomata respond directly to air humidity, resulting in higher stomatal conductance in conditions of low vapour pressure deficit. Numerous studies with different species (*Corylus maxima* Mill., *Rosa hybrida* L., *Lycopersicon esculentum* Mill.) have demonstrated that under high relative air humidity (RH), fully grown plants possess malfunctioning stomata that are no

longer able to close in response to stimuli such as darkness, abscisic acid (ABA) or desiccation (Fordham et al., 2001; Arve et al., 2013; Fanourakis et al., 2013; Arve and Torre, 2015). This indicates that high levels of RH can override signals from periods of darkness (Arve et al. 2013). Furthermore, Aliniaiefard et al. (2014) demonstrated that a single environmental factor, high air humidity, had the strongest negative effect on stomatal closing response and the magnitude of stomatal malfunctioning. Mott and Parkhurst (1991) proposed that stomata respond to air vapour pressure deficit (VPD) via the transpiration rate rather than humidity *per se*. It is surprising that a single environmental factor – air humidity – can affect the network of stomatal control (Aliniaiefard and van Meeteren, 2013; Aliniaiefard et al., 2014).

Numerous studies have shown that the main driving force of night-time transpiration is either VPD (Bucci et al., 2004; Rogiers et al., 2009; Zeppel et al., 2010, 2011) or a combination of VPD and wind speed (Benyon 1999, Daley and Phillips, 2006). It is commonly reported that the night-time sap flow of woody species is positively associated with VPD (Zeppel et al., 2010, 2011). Therefore, night-time water loss is widespread in warm, dry environments, with high night-time VPD. Similarly, soil water content is positively correlated with night-time stomatal conductance (Dawson et al., 2007; Zeppel et al., 2010, 2011). Zeppel et al. (2011) found that night-time and daytime sap flow respond in similar ways to VPD and soil water content. In contrast, Ogle et al. (2012) found differential daytime and night-time stomatal behaviour to VPD and soil water potential in plants from North American deserts, suggesting that different mechanisms underlie daytime and night-time stomatal regulation.

Recent studies in a Free Air Humidity Manipulation (FAHM) experimental site have shown that long-term increase in daytime RH and a concomitant rise in soil water content trigger diminished canopy water flux in deciduous tree species (Kupper et al., 2011; Sellin et al., 2017). Reduced water flux may in turn reduce the transpiration-driven mass flow of nutrients in the soil and potentially lead to diminished nutrient supply to the foliage (Tullus et al., 2012; Sellin et al., 2013). In the FAHM experiment, elevated RH caused higher stress in trees by disturbing starch accumulation and carbohydrate and N metabolism and through restricting both photosynthetic capacity and tree growth rates (Tullus et al., 2012; Sellin et al., 2013, 2017; Rosenvald et al., 2014). Although several studies have investigated plant mineral nutrient uptake and concentrations under elevated RH, the results have been rather controversial (Leuschner 2002; Lihavainen et al. 2016; Sellin et al. 2017).

1.5 Aims of the thesis

Night-time stomatal regulation and water relations have been studied in different plant species during the last two decades. Nevertheless, no commonly accepted mechanism exists for stomatal regulation during periods of darkness (Merilo et al., 2014; Zeppel et al., 2014). It is a well-known fact that plants with

high daytime stomatal conductance tend to demonstrate higher night-time stomatal conductance and transpiration rates (Snyder et al., 2003; Caird et al., 2007). However, night-time stomatal opening and water relations may be highly dependent on several endogenous factors, including foliar nutrient concentration (Resco de Dios et al., 2013). Nevertheless, previous findings regarding the effects of environmental variables such as soil mineral nutrient availability and air humidity on endogenous night-time water flux and gas exchange are controversial. Therefore, a greater understanding of the environmental factors responsible for the regulation of night-time water loss in woody species is required. The current thesis provides new information regarding the impact of plant endogenous and environmental factors on night-time and predawn water relations and gas exchange in deciduous woody tree species.

The objectives of the thesis are

- To investigate the role of endogenous factors on predawn stomatal opening and night-time water flux (**I–III, V**).
- To elucidate the interactions between night-time water flux and mineral nutrient acquisition (**I–IV**).
- To examine the effect of atmospheric conditions (VPD, wind speed) on night-time water flux (**IV–V**).

2. MATERIALS AND METHODS

2.1 Experimental set-up

Paper I

An experiment with eight 3-year-old micro-propagated hybrid aspen (*Populus × wettsteinii* Hämet-Ahti) saplings was undertaken out in growth chamber Percival AR-95 HIL (Percival Scientific Inc., Perry, IA). The saplings were grown in two different mineral nutrient contents in order to examine the impact of soil nutrient availability on diurnal water flux. The concentration of macro- and micronutrients in the growth substrate (calcimined sphagnum peat) was twice as great in the high nutrient availability (high-n) treatment than in the low nutrient availability (low-n) treatment. In addition, the growth substrate of the high-n treatment was regularly (nine times) enriched with a water-dissolved fertiliser during the growth period. The night/day length in the chamber was 8.5/15.5 h. The average RH and air temperature (T_A) in the growth chambers varied from 65.1–71.3% and 20.6–22.4 °C, respectively.

Paper II

The experiment with cut shoots of 16 deciduous woody species from different habitats in south-eastern Estonia was undertaken under the controlled conditions of growth chamber AR-95 HIL. The aim was to investigate patterns of night-time water use across different tree species. The shoots were cut from individual trees with secateurs and then re-cut with a razor blade under deionised (Direct-Q3 UV water purification system; Millipore SAS, Molsheim, France) and freshly degassed water (T-04-125 ultrasonic-vacuum degasser; Terriss Consolidated Industries, NJ). The shoots were subsequently re-cut under water in the laboratory and inserted into 100 ml plastic flasks filled with deionised and freshly degassed water. The flasks containing the sample shoots were weighed regularly at 21:30, 05:30, 09:30 and 14:30 h (Table 1) to estimate shoot water loss for different time periods. The average shoot water loss was calculated for four different time periods: 'night' (from 21:30 to 05:30 h), 'artificial predawn' (from 05:30 to 09:30 h), 'night and artificial predawn' (from 21:30 to 09:30 h) and 'daytime' (from 09:30 to 14:30 h) (Table 1). Dark respiration (R_d ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and night-time leaf conductance to water vapour (g_{ap} ; $\text{mmol m}^{-2} \text{s}^{-1}$) were measured from 07:30 to 09:30 h. Net photosynthesis (P_n ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and daytime leaf conductance (g_d ; $\text{mmol m}^{-2} \text{s}^{-1}$) were measured from 14:30 to 16:30 h. The daily photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) inside the growth chamber was kept constant at 450–550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the level of the shoots. The RH was 55.3 and 62.4% at night and during the daytime, respectively. The T_A was 22.5 °C at night and during the day. A timetable of the experiment is given in Table 1.

Paper III

The experiment with hybrid aspen (*Populus × wettsteinii* Hämet-Ahti) cut shoots and saplings was undertaken both in the controlled conditions of a

growth chamber AR-95 HIL and in field conditions, where the xylem sap flow of saplings was measured. The aim was to elucidate the ways in which long-term exposure to increased air humidity affects night-time gaseous phase conductance and gas exchange. The cut shoots were taken from the FAHM experimental site, where the long-term average increase in RH during artificial humidification was ~6–7% units (Sellin et al., 2017). The preparation of shoots for measurement (cutting, transport, re-cutting) in the growth chamber was similar to study **II**. The daily photosynthetically active radiation inside the growth chamber was kept at 450–550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the level of the shoots. The RH was 57.3 and 56.9% at night and during the day, whereas the respective values of T_A were 21.6 and 22.8 °C. The ‘early night’ measurements (leaf conductance, g_{n1} ; dark respiration, R_1) were carried out from 01:00 to 02:30 h, and the ‘artificial predawn’ measurements (g_{n5} , R_5) from 05:00 to 06:30 h. Daytime measurements (g_d , P_n) were carried out from 9:00 to 10:30 h. The timetable of the activities and conditions during the experiment is provided in Table 2.

Paper IV

The experiment with six 4-year-old silver birch (*Betula pendula* Roth.) saplings was carried out under the controlled conditions of a growth chamber AR-95 HIL. The goals of the experiment were to investigate the impact of elevated day-time atmospheric humidity on diurnal water flux and mineral nutrient uptake. The growth substrate of trees was characterised by high mineral nutrient content. The impacts of two different air humidity regimes on seedling growth were compared: (1) high daytime and night-time air humidity (H treatment) and (2) moderate daytime and high night-time air humidity (M treatment). The daytime RH was ~15% higher in the H treatment (77.4%) than in the M treatment (61.7%), whereas the night-time RH did not differ between the treatments. During the study the night/day length in the chamber was 8/16 h, whereas the daily photosynthetically active radiation was held 400–700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the upper foliage.

Paper V

The experiment was conducted on intact branches and sample shoots of 7-year-old saplings of five fast-growing deciduous tree species (*Alnus incana* (L.) Moench, *Alnus glutinosa* (L.) Gaertn, *Betula pendula* Roth., *Populus tremula* L., and *Populus × wettsteinii* Hämet-Ahti). The branch sap flow was recorded in intact branches of 20 sample trees in the FAHM experimental area and leaf gas exchange measurements in cut shoots were conducted in a growth chamber AR-95 HIL. The aim was to investigate the responses of night- and daytime water fluxes to environmental stimuli and endogenous drivers in tree species with different water-use strategies. The preparation of shoots for measurements (cutting, transport, re-cutting) in the laboratory was similar to studies **II** and **III**. The daily photosynthetically active radiation in the chamber was kept at 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the level of the shoots. The RH and T_A were kept steadily at 60% and 23 °C, respectively.

Table 1. Timetable of activities and conditions during the experiment of the **II** paper.

Natural sunset 21:38–21:16		Natural sunrise 05:00–05:20	
Natural night		Natural night	
Preparation of shoots for measurement (cutting, transport, re-cutting)			“Artificial predawn” gas exchange measurements
			“Daytime” gas exchange measurements
Darkness in growth chamber		Light in growth chamber	
18:00	21:00	06:00	16:30
	1st weighing	2nd weighing	3rd weighing
			4th weighing

Table 2. Timetable of activities and conditions during the experiment of the III paper.

Natural sunset 22:05–21:52		Natural sunrise 04:31–04:46	
Preparation of shoots for measurement (cutting, transport, re-cutting)		„Early night“ measurements	„Artificial predawn“ measurements
19:00		Light in growth chamber	
20:00	21:00	22:00	23:00
Darkness in growth chamber			
01:00	02:00	03:00	04:00
05:00	06:00	07:00	08:00
09:00	10:00	Light in growth chamber	

2.2 Water relations and gas exchange measurements

The xylem sap flow of saplings was measured with a T4.2 sap flow system (EMS Brno, Brno, Czech Republic) equipped with 'Baby Kucera' sap flow sensors (**I**, **III–V**). In order to express the daytime (F_d ; $\text{mmol m}^{-2} \text{s}^{-1}$) and night-time (F_n ; $\text{mmol m}^{-2} \text{s}^{-1}$) sap flux density per unit of the projected leaf area, the total leaf area of saplings (A_L ; cm^2) was determined using optical area metres LI-3000C and LI-3100C (Li-COR Biosciences, Lincoln, NE). Whole tree canopy conductance to water vapour (**III–IV**) (g_c ; $\text{mmol m}^{-2} \text{s}^{-1}$) was computed from the data of sap flux density (F) using a simplified Penman-Monteith equation:

$$g_c = (F \times P) / \text{VPD}_L \quad (1)$$

where P is atmospheric pressure (kPa) and VPD_L is the vapour pressure difference between leaf and atmosphere (kPa) calculated from the data of RH, T_A and leaf temperature.

In study **II** the average water loss was expressed per unit leaf area to determine shoot transpiration rates (E ; $\text{mmol m}^{-2} \text{s}^{-1}$). In order to estimate the shoots' relative ability to use water at night, the night-time water use percentage from daytime water use (NWU; %) was calculated as the proportion of mean night-time water flux in comparison to mean daytime water flux (**I–II**). In order to estimate the predawn stomatal opening, the increase in shoot night-time transpiration rate (INT; %) was calculated from the data of night-time (E_n) and artificial predawn (E_{ap}) transpiration rates (**II**).

In studies **II** and **III** the leaf water potential (Ψ_L ; MPa) was measured via the balancing pressure technique (Boyer, 1995; Holbrook et al., 1995) using a Scholander-type pressure chamber after gas exchange measurements. In experiment **III** the whole shoot hydraulic conductance (K ; $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) was calculated from the leaf transpiration rate (E ; $\text{mmol m}^{-2} \text{s}^{-1}$) and water potential gradient between the leaf and pure deionised water in the flask ($\Delta\Psi$; MPa):

$$K = E / \Delta\Psi \quad (2)$$

The gas exchange measurements were undertaken using a portable gas exchange system (CIRAS-2; PP-Systems, Amesbury, MA) inside the growth chamber of one (**II**) or three fully expanded leaves (**III**, **V**) per sample shoot. Gas exchange measurements were carried out at constant irradiance (0 and 500–700 $\mu\text{mol m}^{-2} \text{s}^{-1}$, at night and in the daytime, respectively), cuvette temperature (22–23 °C), external CO_2 concentration (370–380 ppm) and ambient air humidity of the chamber.

2.3 Data analysis

Statistical data analyses were carried out using the software Statistica, Version 7.0 (StatSoft Inc., Tulsa, OK). A repeated measures analysis of variance (ANOVA) was applied to the datasets in order to analyse the dynamics of sap flux density (F) (**I**), night-time water use percentage (NWU) (**I**) and canopy conductance (g_c) (**IV**) between the treatments during the study period. A Student's t-test for dependent samples was used to estimate the following: changes in sap flux density (F) at night (**I**); differences between night- and daytime transpiration rates and leaf conductance (**II**); and differences in leaf conductance (g), shoot hydraulic conductance (K), shoot transpiration rate (E) and leaf water potential (Ψ_L) between the treatments (**III**). In study **II**, a Student's t-test for independent samples was applied to various parameters in order to estimate the differences between species. The assumptions of normality and homogeneity of variance were checked using the Kolmogorov-Smirnov test and the Levene test, respectively. In study **III**, a Mann-Whitney U test for independent samples was applied to various measured parameters in order to estimate differences between early night and predawn. A simple linear regression analysis was carried out to assess bivariate relationships between dependent and predictor variables (**I–III**, **V**). The normality of the regression residuals was checked using the Kolmogorov-Smirnov D-statistic (**I**, **III**, **V**) or Shapiro-Wilk test (**II**). If the normality of residuals was not met, a log-transformation procedure was conducted.

3. RESULTS AND DISCUSSION

3.1 Factors affecting endogenous stomatal opening (I-III, V)

Hybrid aspen (*Populus × wettsteinii*) saplings grown in high nutrient availability (high-n) treatment demonstrated considerable variability in sap flux density (F) during the night-time period (I). Sap flux density significantly increased from 5:00 to 7:00h ($P < 0.05$) in the high-n treatment, but not with the low nutrient availability (low-n) treatment (Fig. 1). Such an endogenous increase in F during the predawn hours was most likely caused by the gradual opening of the stomata. An endogenous, gradual increase in the stomatal opening before dawn has also been described in many other plant species from different environments (Bucci et al., 2004; Dodd et al., 2005; Howard and Donovan, 2007; Resco de Dios et al., 2012, 2013). The endogenous timer of plant metabolism controls the temporal pattern of transcription in photosynthesis, stomatal opening, and other physiological processes (Hubbard and Webb, 2015). Furthermore, circadian regulation may support the uptake of nitrate and ammonium from the soil as night-time water flux facilitates the avoidance of an accumulation of different soluble nitrogen compounds in fine roots that may inhibit nitrate and ammonium uptake (Gessler et al., 1998, 2002).

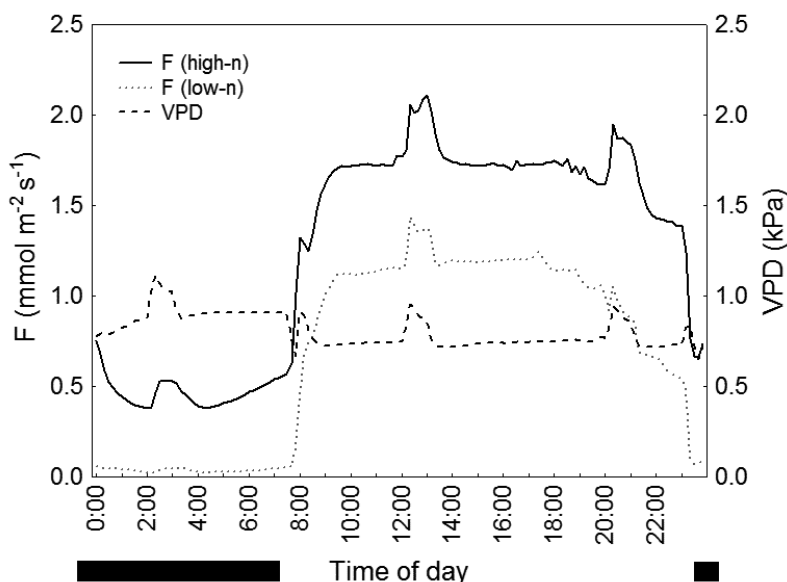


Figure 1. Average daily course of the stem sap flux density (F) in high nutrient availability treatment (high-n) and low nutrient availability treatment (low-n) and air vapour pressure deficit (VPD) in growth chamber during period of sap flow measurements. Both lines of the F represent the average value of four measured trees. The line of the VPD represents the average value in the growth chamber. The black strip expresses night-time.

In the growth chamber experiment with 16 deciduous woody species (Table 1 in **II**) from various habitats (**II**), more than a half (10 out of 16) of all species appeared to increase the aperture of their stomata prior to dawn (Fig. 2). Furthermore, the species (*Populus × wettsteinii*, *Frangula alnus* Mill. and *Alnus glutinosa*) that demonstrated a significant increase in shoot night-time transpiration rates at artificial predawn (INT) exhibited a superior foliar nitrogen concentration. The results are consistent with previous studies, which have shown a substantial endogenous increase in stomatal opening during the predawn period in several fast-growing tree species such as *Populus angustifolia* James and *Eucalyptus camaldulensis* (Howard and Donovan, 2010; Resco de Dios et al., 2016). High predawn stomatal conductance could constitute an adaptive response, but it may reduce diffusional limitation to photosynthesis during the early daylight hours and thus increase carbon fixation (Oren et al. 1999; Daley and Phillips 2006; Caird et al. 2007). Indeed, Resco de Dios et al. (2016) demonstrated that intensive predawn stomatal conductance promoted increased carbon assimilation and enhanced growth across six different *Eucalyptus camaldulensis* genotypes shortly after dawn. Nevertheless, predawn stomatal conductance only has a minimal effect on early-morning photosynthesis for a few minutes following dawn in *Helianthus annuus* plants (Auchincloss et al., 2014). Nonetheless, the temporal pattern of nocturnal stomatal conductance is largely regulated by the circadian clock, which may affect plant photosynthetic carbon gain by preopening stomata before dawn. These findings are consistent with a previous study involving hybrid aspen (**I**), which demonstrated a substantial increase in predawn water flux in saplings with more intensive growth.

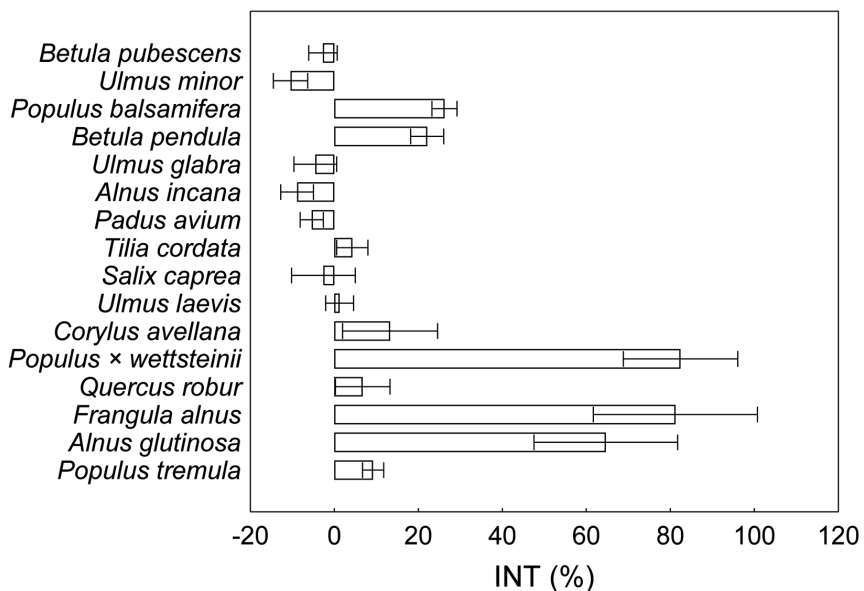


Figure 2. Average increase in shoot night-time transpiration rate at artificial predawn (INT) in 16 deciduous tree species. Bars represent standard error of the mean.

Night-time gas exchange in hybrid aspen (*Populus × wettsteinii*) grown at elevated air humidity also varied considerably during the night (III). The predawn leaf conductance (g_{n5}) was 2.7 times higher ($P < 0.001$) than early night leaf conductance (g_{n1}) in the humidification (H) treatment (Fig. 3). Indeed, the temporal pattern of nocturnal stomatal conductance, primarily driven by circadian rhythms, is often characterised by diminished stomatal conductance in the initial hours of darkness, followed by significant increases later in the night, and reaching a peak immediately before the dawn (Hennessey et al., 1993; Resco de Dios et al., 2013, 2015). In the H treatment, predawn shoot hydraulic conductance (K_s) also achieved maximum values in darkness. It is plausible that shoot hydraulic conductance in darkness could be regulated by aquaporin water channels, which are modulated by environmental stimuli and the circadian clock (Takase et al., 2011; Li et al., 2013). Moreover, leaf dark respiration at elevated air humidity increased during the night-time (III). However, at ambient air humidity, dark respiration decreased towards dawn, indicating that the quantity of respiration substrates (starch and soluble sugars) probably declined. It is a common rule that the starch pool is almost completely exhausted by the end of the night (Suplice et al., 2009). Given that the height growth of aspen sprouts was significantly ($P < 0.01$) higher under ambient than under humidified conditions, it is likely that trees at ambient air humidity were better able to convert the carbon products of starch degradation into growth than were the trees at elevated air humidity, whose demand for carbohydrates for growth was probably smaller. If sucrose export at night is restricted by low demand from sink organs, sucrose accumulates in the leaves and trehalose 6-phosphate (sugar-signalling metabolite) content rises, leading to the inhibition of an early step in the pathway of starch degradation (Martins et al., 2013). We assume that the increase in leaf conductance and dark respiration in the H treatment during predawn might be caused by the accumulation of soluble sugars, the concentration of which correlates with dark respiration level (Lewis et al., 2011). Furthermore, Lihavainen et al. (2016) demonstrated that the humidification treatment affected the carbohydrate and nitrogen metabolism of silver birch and hybrid aspen in the FAHM experiment. Therefore, we suggest that intensive predawn stomatal conductance and increasing dark respiration at the end of the night may reflect a form of plant stress response to altered carbohydrate metabolism.

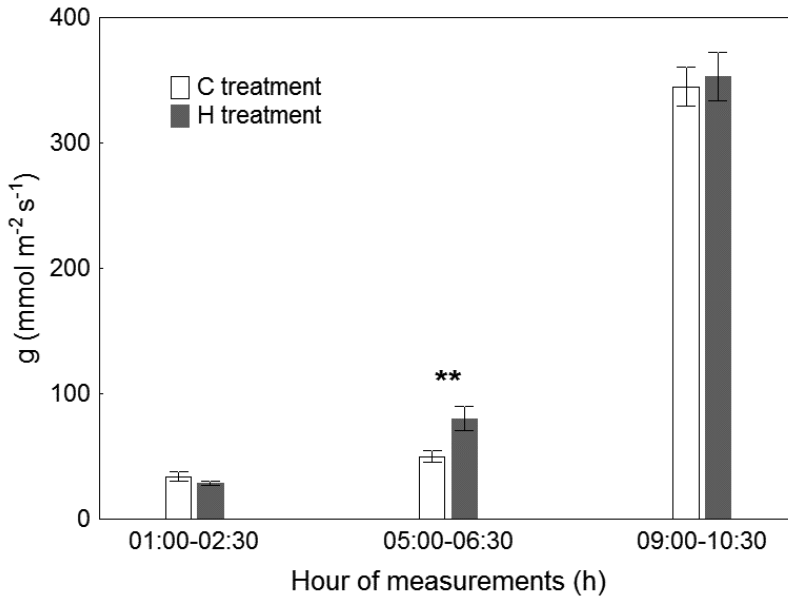


Figure 3. Average leaf conductance (g) in control (C) and humidification (H) treatments in three different time periods: early night (01:00–02:30 h), predawn (05:00–06:30 h) and daytime (09:00–10:30 h). The error bars represent the standard error around the mean. The significance of the differences between the treatments was estimated using the Student's t test. * $P < 0.05$; ** $P < 0.01$

In study V, both predawn stomatal conductance and dark respiration rate were significantly correlated with predawn leaf sucrose content (Fig. 4). These findings support the idea of paper III, that nocturnal gas exchange is related to the content of soluble sugars. It is widely acknowledge that sucrose is an important osmoticum, which is actively involved in guard cell turgor regulation via blue light-induced cell membrane polarisation at dawn and in daylight (Lasceve et al., 1997; Talbott & Zeiger, 1998). Furthermore, starch metabolism may directly affect endogenous predawn stomatal opening by providing osmoticans (soluble sugars) for stomatal regulation (Easlon and Richards, 2009). Starch accumulates in the light and is degraded at night to support continued respiration for energy supply and to provide carbon for growth (Suplice et al., 2009; Geigenberger, 2011).

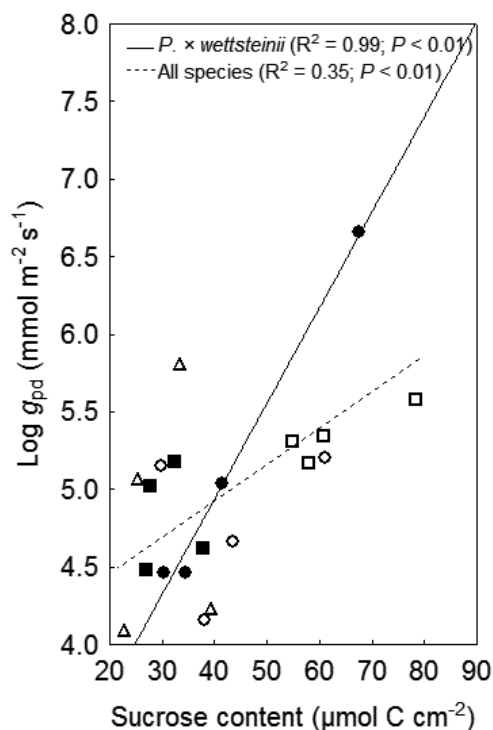


Figure 4. Relationships between log-transformed predawn stomatal conductance (g_{pd}) and leaf sucrose content. From individual species, the relationship was statistically significant only in *Populus × wettsteinii*.

3.2 Interactions between night-time water flux and mineral nutrient acquisition (I-IV)

The soil mineral nutrient deficiency influenced night-time water flux in saplings of hybrid aspen (I), whereas the basic limiting element in the low nutrient availability treatment was nitrogen. Both the night-time sap flux density (F) and night-time water use percentage from daytime water use (NWU) were several times higher in fertilised soil compared to nutrient deficiency ($P < 0.01$). Furthermore, NWU was closely associated with high foliar N concentration ([N]). However, an endogenous increase in F was only observed in nutrient-rich soils, and not in trees grown under nutrient deficiency. It is known that endogenous patterns of night-time stomatal opening, as reflected in leaf conductance, are affected by the photosynthetic conditions of the previous day (Easlon and Richards, 2009). Therefore, it is possible that in nutrient deficiency-grown trees, diminished photosynthesis due to nitrogen and phosphorous limitation resulted in diminished night-time stomatal opening the following night. Several studies have shown that night-time stomatal openness and transpiration are typical of fast-growing, shade-intolerant pioneer species (Daley and Phillips, 2006; Marks

and Lechowicz, 2007), which have relatively high growth rates and leaf nitrogen concentrations. Thus, high growth rates and leaf [N] are more plausible amongst hybrid aspen trees growing in fertile (and well-watered) soils than under conditions of nutrient deficiency. However, increased night-time transpiration in response to nutrient availability is likely to be of a species-specific nature, whereas night-time leaf conductance affected responses to nutrients as well as among life forms and ecological strategies (Caird et al., 2007).

The patterns of night-time water use in 16 woody species varied in their relationships with leaf nitrogen concentration (**II**): shoots with high NWU were characterised by significantly ($P < 0.05$) lower [N], whereas shoots with the highest INT demonstrated greater [N] (Fig. 5). Thus, the species characterised by low [N] transpired more (relatively) at night, whereas species with high [N] opened their stomata before dawn more intensively. Furthermore, the INT and NWU were inversely related to each other ($R^2=0.31$; $P<0.05$); thus, species with lower NWU demonstrated higher INT. We assumed that limited nitrogen availability could stimulate night-time stomatal conductance or transpiration rates relative to daytime. Our findings are consistent with the results of Scholz et al. (2007), who demonstrated that unfertilised savannah trees exhibited higher nocturnal water use and stomatal conductance than did nitrogen-fertilised trees. However, in their experiment the fertilised trees probably suffered under secondary water stress. The relatively high night-time transpiration in trees characterised by low leaf [N] may enhance the delivery of nutrients to the absorbing surfaces of roots via the mass flow of water (Cramer et al., 2008), or may support the xylem-loading of different nitrogen compounds (Gessler et al., 2002). It is likely that relatively high night-time transpiration rates may enhance the uptake of mineral nutrients such as nitrate from the soil (Snyder et al., 2003). Although in study **I** we found the highest values of NWU in the high-n treatment, it is likely that the mechanisms responsible for nitrogen acquisition under nutrient deficiency are different in fertile conditions. Furthermore, the species that are adapted to grow in fertile soils may not possess the mechanisms that allow them to compensate their low N availability via continuous night-time transpiration flux. Nevertheless, the species with high leaf [N] exhibited an endogenous increase in shoot night-time transpiration rate during the predawn hours (**II**). Such an increase in stomatal opening before dawn is likely to be contingent on [N], which determines plant photosynthetic capacity and accumulation of carbohydrates (Lewis et al., 2011).

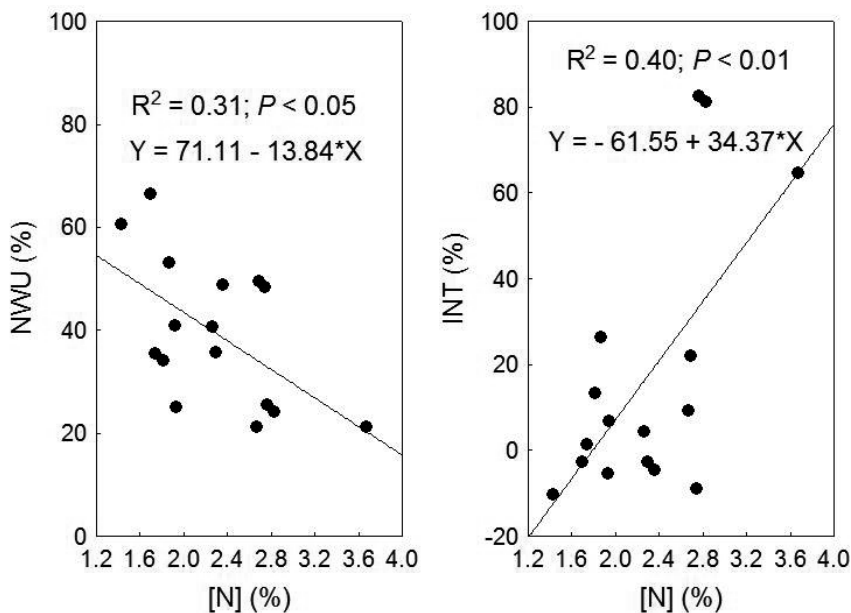


Figure 5. Relationships between shoot water use (shoot night-time water-use percentage of daytime water use, NWU; increase in shoot night-time transpiration rate in artificial predawn hours, INT) and leaf nitrogen concentration ([N]).

In study **III** the leaf nutrient concentration and transpiration rate (except in predawn) did not differ between the treatments. However, the leaf nitrogen content was positively related ($P < 0.05$) to predawn leaf conductance under ambient conditions, whereas the relationship was not significant in trees grown at elevated air humidity. This was probably caused by altered carbohydrate and nitrogen metabolism under humidification (Lihavainen et al., 2016). In study **IV**, neither the foliar N concentration nor content differed between the high and moderate air humidity treatments, which was probably due to the very high soil nitrogen concentration. Nevertheless, the total P content was 32.3% higher at elevated air humidity-grown trees than under moderate daytime air humidity conditions. The trees grown at elevated air humidity took up 28.2% more water than did the trees under moderate daytime air humidity conditions, whereas 43.3% of this additional amount of water was consumed during the night (Fig. 6). Therefore, we propose that higher foliar P content in humidity-treated trees might be related to higher transpiration-driven mass flow and/or by a 25.4% greater number of absorptive root tips. Although the P concentration in soil solutions in natural conditions is typically very low and is taken up via diffusion and interception by mycorrhizae (Cramer et al., 2009), the mass flow of P can be substantial in fertilisation experiments with a mass flow of mobile P forms (Cramer et al., 2008). In our study, the soil P existed in an easily available and water-soluble form (phosphorous pentoxide), which is likely to move readily with mass flow.

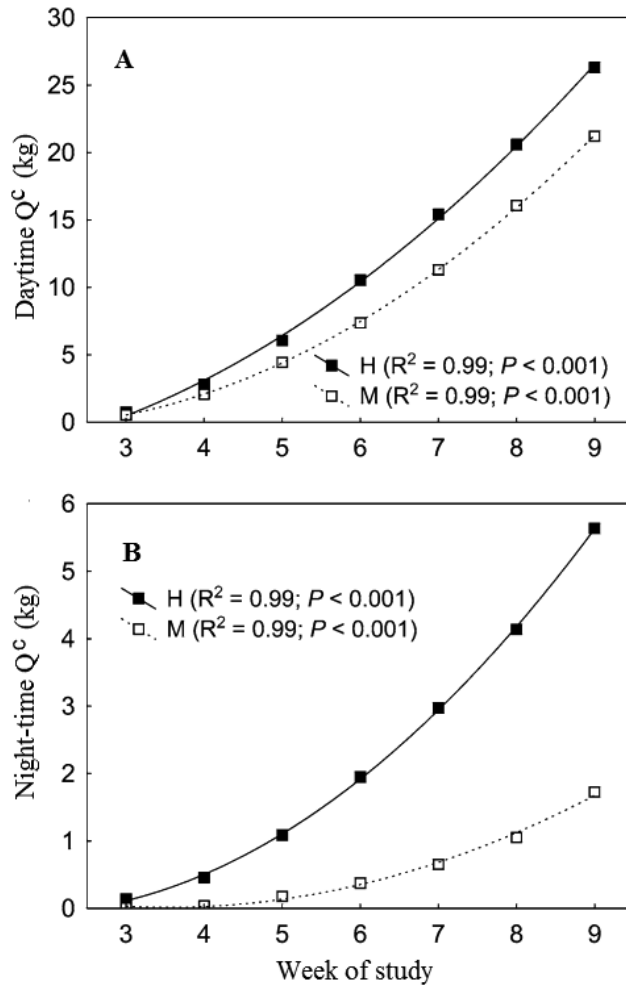


Figure 6. Relationships between dependent variables: **(A)** daytime cumulative sap flow (Q^c), **(B)** night-time Q^c and predictor variable (week of study) in high (H) and moderate (M) air humidity treatments. Values of R^2 and P were obtained from polynomial regression analyses

3.3 Effects of air humidity on night-time water flux and gas exchange (III-V)

In our experiment with hybrid aspen grown at ambient and elevated air humidity conditions **(III)**, canopy conductance (g_c) sensitivity to VPD_L did not differ between the treatments either at night or during the day (Fig. 7). This finding does not accord with earlier studies showing that plants grown under high air humidity are more insensitive to water loss than are plants grown at moderate RH (Arve et al., 2013; Aliniaiefard et al., 2014). Furthermore, the

leaves of several C3 species exhibit reduced control of water loss, owing to their less functional stomata under long-term high RH (Fanourakis et al., 2013; 2016). However, the trees in our experiment were not humidified at constantly high RH as in the aforementioned studies, which may explain why we could not observe differences between the two treatments. Nevertheless, it has been shown that the effects on transpiration rates of low VPD can have different causes depending on the length of exposure time of leaves to low VPD.

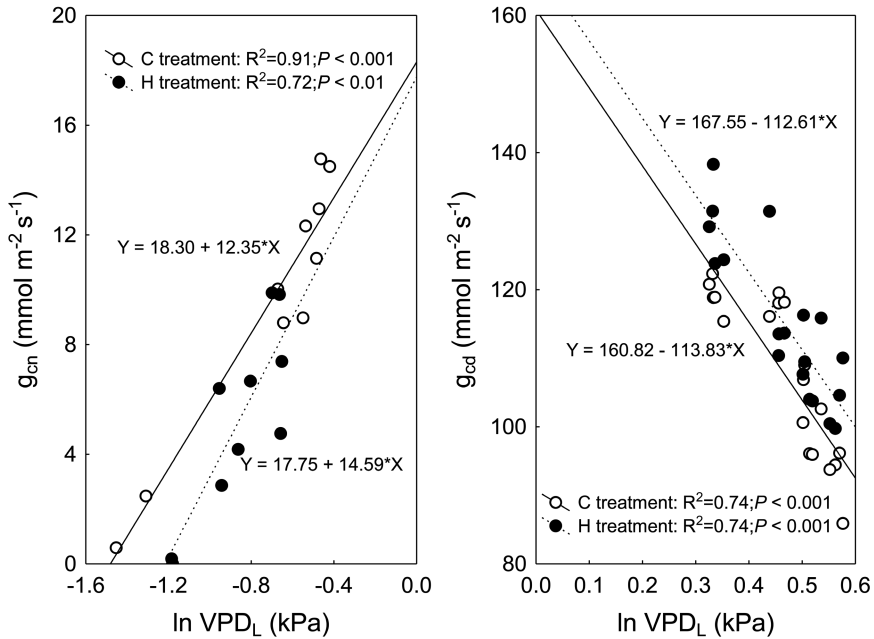


Figure 7. Relationships between canopy conductance (night-time, g_{cn} ; daytime, g_{cd}) and log-transformed vapour pressure difference between leaf and atmosphere (VPD_L) in the control (C) and humidification (H) treatment in humidification-free conditions. Values of R^2 and P have been obtained from simple regression (type III) analysis.

In growth chamber experiment with *B. pendula* trees, elevated daytime atmospheric humidity increased the potential for night-time water flux (IV). A ~40% lower daytime VPD_L caused significantly higher night-time canopy conductance to water vapour (g_c) in silver birch trees in spite of similar night-time VPD_L between the two treatments (Fig. 1 in paper IV). Our results clearly demonstrate that silver birch saplings can regulate night-time water flux according to the RH experienced during the daytime. The superior night-time canopy conductance in trees grown at higher air humidity conditions was probably induced by a lower tissue abscisic acid (ABA) concentration, which is an important stress hormone that induces stomatal closure. It has previously been shown that ABA content was lower under high RH in comparison to lower RH (Nejad and van Meeteren 2007; Arve et al., 2013; Aliniaefard et al., 2014), whereas low ABA levels

contribute to the development of malfunctioning stomata, resulting in high water loss during desiccation and reduced dark-induced stomatal closure. This is consistent with previous studies, which have shown that an increase in ABA levels during the dark period in a lower RH act as a signal for stomatal closure in darkness (Tallman 2004; Novakova et al., 2005; Arve et al., 2013).

In our experiment with five fast-growing tree species air vapour pressure deficit (VPD) and wind speed were the main drivers of night-time and daytime water flux in all studied species (V). It is known that the most commonly reported environmental drivers of nocturnal water fluxes are air vapour pressure deficit (VPD), soil water content and wind speed, whereas the primary environmental factor driving night-time water loss is atmospheric evaporative demand (Caird et al., 2007; Dawson et al., 2007; Zeppel et al., 2014). Nevertheless, in our study (V), wind speed explained a major part of the total variation in night-time sap flux density in *A. glutinosa* and explained some of the variation of night-time water flux in *P. × wettsteinii*, *P. tremula* and *B. pendula*. Similarly, previous studies have shown that wind speed may substantially affect night-time water loss in various tree species (Phillips et al., 2010; Karpul and West, 2016), including *B. pendula* (Sellin and Lubenets, 2010). Furthermore, Phillips et al. (2010) found that wind speed is a more important driver of night-time water flux than VPD in *Eucalyptus* species. This is consistent with our results in *A. glutinosa*, which is characterised by large leaves and therefore has high boundary layer resistance to transpiration. Thus, leaf size and morphological traits may have an important impact on a tree's ability to lose water at night.

4. CONCLUSIONS

The following conclusions can be drawn based on this thesis:

1. Leaves with high nitrogen concentration (both within and across the species studied) demonstrated a significant increase in night-time transpiration rate during predawn. Such circadian regulation of stomatal opening may promote increased carbon assimilation early in the morning.
2. Growth under conditions of elevated air humidity affected the predawn stomatal regulation of hybrid aspen, whereas stump sprouts grown at elevated air humidity opened their stomata more efficiently in artificial dawn. The higher predawn leaf conductance was likely caused by altered carbohydrate metabolism of the humidified trees with slower growth rate.
3. Leaves' sucrose content is related to predawn stomatal opening in hybrid aspen. Thus, in fast-growing species like hybrid aspen sucrose is probably involved in modulating the night-time stomatal regulation.
4. The species with low leaf nitrogen concentration lost relatively more water at night than during the daytime. This could potentially compensate limited nitrogen uptake in species able to grow in nutrient-poor habitats.
5. Elevated daytime atmospheric humidity increased the potential for night-time water flux and might also facilitate the uptake of water soluble mineral nutrients which can probably move readily with mass flow.
6. Air vapour pressure deficit (VPD) and wind speed were the main drivers of night-time water flux. The wind speed was an even more important driver of night-time sap flow than VPD in species that are characterised by leaves with high boundary layer resistance to transpiration. Thus, leaf morphological traits may impact trees ability to loose water at night.
7. Current results indicate that nightly and daily stomatal responses to VPD are species-specific and may greatly differ even between congeneric species.

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SUMMARY IN ESTONIAN

Taimesiseste- ja keskkonnategurite mõju heitlehiste puuliikide öisele veevahetusele

Paljud, erinevates ökosüsteemides kasvavad puit- ja rohttaimed transpireerivad öösel tänu mittetäielikult sulgunud õhulõhedele. Sealjuures moodustab öine transpiratsioon enamasti 5–30% päevasest veevoost. Peamised transpiratsiooni mõjutavad keskkonnategurid on õhuniiskus, õhu temperatuur, tuule kiirus ja valguse intensiivsus, aga ka mulla vee- ning mineraaltoitainete sisaldus. Päevase ja öise transpiratsiooni liikumapanevaks jõuks on veeauru rõhu defitsiit (VPD), mis otseselt sõltub nii suhtelisest õhuniiskusest kui ka välisõhu temperatuurist. Õhuniiskuse suurenedes väheneb veeauru rõhu defitsiit, mistõttu õhulõhed sulguvad, vähendades sellega nii veekadu kui ka gaasivahetust taime lehe ja atmosfääri vahel. Suurimad öised veekaod on iseloomulikud just kuiva ja sooja kliimaga piirkondades, kus öine VPD on kõrge.

Öine õhulõhede avatus (ja seeläbi transpiratsiooni intensiivsus) sõltuvad ka mulla mineraaltoitainete sisaldusest. Suhteliselt intensiivne öine veetransport on taimedele iseloomulik just lehestiku aktiivse kasvu perioodil kui nõudlus lämmastiku ja teiste makroelementide järele on tavapärasest suurem. Tõenäoliselt võib öine transpiratsioon aidata taimedel paremini omastada mullast mineraaltoitaineid ning ei saa välistada võimalust, et puittaimede öine transpiratsioon on suhteliselt intensiivsem vähese toitainete sisaldusega kasvukohtades. See võimaldaks suurendada mobiilsete toitainete (sh. nitraatlämmastiku) liikuvust mullas massivoolu abil juurteni ning soodustada taimesisest mineraalelementide transporti juurtest lehtedesse. Siiski, öine transpiratsioon ei varieeru ainult tulevalt keskkonnategurite mõjust, vaid tingituna ka füsioloogilisest erinevusest nii liikide vahel kui ka liikide siseselt.

Kuigi käesoleval sajandil on laialdaselt uuritud keskkonnateguritest tingitud öist õhulõhede regulatsiooni ja veevahetust erinevatel taimeliikidel, ei ole leitud ühest mehhanismi, mis reguleerib öist õhulõhede avatust. Mitmed senised uuringud näitavad, et suurema päevase õhulõhede juhtivusega taimed omavad ka suuremat juhtivust öösel. Siiski on tänaseni jäänud ebaselgeks, kas ja mil määral võivad erinevad keskkonnategurid mõjutada õhulõhede (sh. endogeenset) regulatsiooni pimedas. Käesolev töö annab ülevaate, kuidas nii keskkonnast tulenevad kui ka taimesisesed tegurid mõjutavad öist ning koidueelset vee- ja gaasivahetust heitlehistel puuliikidel.

Töö eesmärgiks oli:

- Uurida endogeensete ja väliskeskkonna tegurite mõju pimedas aja õhulõhede regulatsioonile ja veevahetusele.
- Analüüsida taimede öise veekasutuse ja mineraaltoitumise vahelisi võimalikke seoseid.
- Teha kindlaks, kuidas mõjutavad atmosfääri tingimused (õhuniiskus, tuule kiirus) pimedas aja veevoogusid erinevatel puuliikidel.

Doktoritöö tulemused näitasid, et paljud heitlehised puuliigid avavad oma õhulõhed koidueelsel ajal, suurendades sellega oluliselt koidueelse transpiratsiooni osatähtsust. Puuliigid (*Populus × wettsteinii*, *Frangula alnus* Mill. ja *Alnus glutinosa*), mis transpireerisid koidueelsel ajal intensiivsemalt, omasid ka suuremat lehe lämmastiku kontsentratsiooni. Saadud tulemustest võib järeldada, et koidueelne õhulõhede avanemine sõltub lehe lämmastiku sisaldusest, määrates sellega taimede fotosünteesilise võimekuse. Õhulõhede avanemine enne koitu võimaldab taimedel siduda süsinikku juba varajastel hommikutundidel, tagades taimedele konkurentsieelise eelkõige kasvukohtades, kus lämmastiku kättesaadavus ning taimede konkurents valguse pärast on kõrge.

Pikaajaline kõrgem suhteline õhuniiskus mõjutab hübriidhaava (*Populus × wettsteinii* Hämet-Ahti) õist kui ka vahetult koidueelset gaasi- ja veevahetust: kõrgema õhuniiskusega keskkonnas kasvanud puud avasid õhulõhed suuremal määral enne koitu, võrreldes mõõduka õhuniiskuse tingimustes kasvanud puudega. Suure tõenäosusega on suurem koidueelne õhulõhede juhtivus seotud muutustega süsivesikute ainevahetuses ja tingitud lahustuvate suhkrute ehk õhulõhede regulatsioonil osalevate oluliste osmootikumide sisalduse suurenemisest. Seda kinnitab ka katse, mis näitas koidueelse õhulõhede juhtivuse ja hingamise positiivset seost koidueelse sahharoosi sisaldusega lehtedes. Doktoritöö tulemusi toetavad ka varasemad uuringud FAHM katsealalt, kus on leitud, et suurenenud õhuniiskus mõjutab süsivesikute ainevahetust arukasel ja hübriidhaaval. Doktoritöö tulemused kinnitavad, et suhkrud on olulised osmootikumid, mis moduleerivad ööpäevast õhulõhede avatust, ning et suurenev atmosfääri suhteline niiskussisaldus võib põhjustada endogeenseid muutusi kiirekasvulise hübriidhaava öises veevahetuses.

Doktoritöö tulemused näitasid, et mulla mineraaltoitainete kättesaadavus mõjutab hübriidhaava õist veevahetust. Hübriidhaab (kui kiirekasvuline heitlehine puuliik) transpireerib öösel intensiivsemalt toitaineterikkal mullal. Intensiivne öine veevoog võib aidata kiirekasvulistel puuliikidel omastada mullast paremini toitaineid, soodustades sel moel kiiremat kasvu, et olla edukam valguskonkurentsis. Öise transpiratsiooni osatähtsus (päevasega võrreldes) näib olevat seotud ka lehtede mineraaltoitainete sisaldusega. Katse erinevate puuliikidega näitas, et madala lehe lämmastiku sisaldusega liigid transpireerivad öösel suhteliselt intensiivsemalt kui päeval ajal. Saadud tulemuste põhjal võib järeldada, et suurem öine veekasutus võib olla kohastumus kasvuks toitainetevaestel muldadel.

Doktoritöö tulemused näitasid, et kõrgem päevane õhuniiskus võib soodustada õist veevahetust. Kõrgema päevase õhuniiskuse tingimustes kasvanud arukased (*Betula pendula* Roth.) transpireerisid intensiivselt nii öösel kui ka päeval. Sealjuures oli kõrgema õhuniiskuse tingimustes kasvanud puudel 32,3% kõrgem lehestiku fosfori kontsentratsioon, võrreldes tavatingimustes kasvanud puudega. Saadud tulemused näitavad, et kõrgem päevane õhuniiskus suurendab nii õist kui päevast veevoogu, mis omakorda võib soodustada mineraaltoitainete omastamist mullast.

Peamised keskkonnafaktorid, mis mõjutasid viie kiirekasvulise puuliigi (*Alnus incana* (L.) Moench, *Alnus glutinosa* (L.) Gaertn, *Betula pendula* Roth, *Populus tremula* L., and *Populus × wettsteinii* Hämet-Ahti) õist veevoogu, on VPD ja tuule kiirus. Sealjuures tuule kiirus on peamine õise veevoo mõjutaja sanglepal, millele olid iseloomulikud suuremad lehed võrreldes teiste analüüsitud puuliikidega. Seega võib lehe suurus olla (tingituna suuremast piirikihi takistusest) oluline morfoloogiline tunnusjoon, mis mõjutab õise veevoo intensiivsust. Samas, õine ja päevane õhulõhede avanemine tingituna VPD-st on liigispetsiifiline ja võib erineda ka sama perekonna lähedaselt seotud liikidel. Käesolevad tulemused kinnitavad, et õine transpiratsioon ei varieeru ainult tulenevalt keskkonna tingimuste erinevustest, vaid suuresti ka füsioloogilistest erinevustest nii liikide vahel kui ka liikide siseselt.

Kliimamuutuste seisukohalt on oluline teada, kuidas optimeerivad heitlehised puud pidevalt muutuvates keskkonnatingimustes oma õist vee- ja gaasivahetust. Pimedal ajal toimuv vee- ja gaasivahetus võib põhjustada muutusi ökosüsteemi ainevoogudes, taimede kasvus ja konkurentsuhetes ning võib seeläbi mõjutada metsaökosüsteemi tootlikkust pikemas perspektiivis. Uusimad teadmised sellest, kuidas ja milliste keskkonnafaktorite poolt on õine ja koidueelne õhulõhede avanemine reguleeritud, võimaldavad senisest paremini selgitada puittaimede kasvu ja talitlust mõjutavaid tegureid ja täpsemalt prognoosida tuleviku kliimamuutuste mõju metsaökosüsteemidele.

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PUBLICATIONS

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birch, a boreal forest tree species. *Regional Environmental Change* **17**: 2149–2157.

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Conference presentations:

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- Kupper P, **Rohula G**, Saksing L, Sellin A, Lõhmus K, Ostonen I, Helmisaari HS, Sõber A. 2012. Does soil nutrient availability influence nighttime water flux of aspen saplings? *Environmental and Experimental Botany* **82**: 37–42.
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