



Circadian patterns of xylem sap properties and their covariation with plant hydraulic traits in hybrid aspen



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ARTICLE INFO

Keywords:

Atmospheric evaporative demand
Circadian patterns
Hydraulic conductance
Osmolality
pH
Potassium ions

ABSTRACT

Physiological processes taking place in plants are subject to diverse circadian patterns but some of them are poorly documented in natural conditions. The daily dynamics of physico-chemical properties of xylem sap and their covariation with tree hydraulic traits were investigated in hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx) in field conditions in order to clarify which environmental drivers govern the daily variation in these parameters. K^+ concentration ($[K^+]$), electrical conductivity (σ_{sap}), osmolality (Osm) and pH of the xylem sap, as well as branch hydraulic traits, were measured in the field over 24-h cycles. All studied xylem sap properties and hydraulic characteristics including whole-branch (K_{wb}), leaf blade (K_{lb}) and petiole hydraulic conductances (K_{p}) showed clear daily dynamics. Air temperature (T_{a}) and photosynthetic photon flux density (PPFD), but also water vapour pressure deficit (VPD) and relative humidity (RH), had significant impacts on K_{wb} , K_{lb} , K_{p} , $[K^+]$ and σ_{sap} . Osm varied only with light intensity, while K_{B} varied depending on atmospheric evaporative demand expressed as T_{a} , VPD or RH. Xylem sap pH depended inversely on soil water potential (Ψ_{s}) and during daylight also on VPD. Although soil water content was close to saturation during the study period, Ψ_{s} influenced also $[K^+]$ and σ_{sap} . The present study presents evidence of coupling between circadian patterns of xylem sap properties and plant hydraulic conductance providing adequate water supply to foliage under environmental conditions characterised by diurnal variation.

1. Introduction

Plants are sessile organisms inhabiting diverse ecosystems; therefore they have to adapt to very different environments. Environmental conditions vary circadianly enormously in most habitats, shaping daily patterns in physiological processes including long-distance water transport. Plants ability to transport water from roots to leaves is essential premise for their growth, competition capacity and survival. Until quite recently xylem was treated as a system of inert pipes constituting a passive pathway for long-distance water transfer in plants. Traditionally it has been presumed that xylem hydraulic conductivity depends on anatomical characteristics of the xylem conduits (Tyree and Ewers, 1991) and transpiration is the driving force pulling water from the soil to leaves, hence creating the water potential gradient within the plant (Cruiziat et al., 2002). One and a half decades ago it was first shown that ionic content of xylem sap can influence hydraulic conductance of xylem in a short time scale (Van Ieperen et al.,

2000; Zwieniecki et al., 2001). There are many papers confirming the ionic effect showing that perfusing branches with KCl or NaCl increases xylem hydraulic conductivity compared to deionized water or other reference solutions (Boyce et al., 2004; Cochard et al., 2010; Nardini et al., 2011, 2012). In light of these findings water transport in plants cannot be considered a purely passive process determined merely by the driving forces and geometry of the conducting system (Nardini et al., 2011; Zwieniecki et al., 2001).

Various mechanisms have been proposed to explain the ionic effect. One of them postulates that ionic effect is caused by shrinking and swelling of pectins in intervessel pit membranes. According to this view enhanced cation content in xylem sap would cause shrinking of pectic matrix increasing nanometric pores in the pit membrane (Nardini et al., 2011; Zwieniecki et al., 2001). Some authors (Cochard et al., 2010) consider this interpretation too simplistic as in some species pit membranes behave such as a gelled non-porous structure. The degree of vessel grouping and intervessel pitting may also contribute to

Abbreviations: A_{L} , foliage area; D_{B} , branch basal diameter; H_{B} , branch height; H_{Brel} , relative branch height; H_{T} , tree height; $[K^+]$, K^+ concentration; K_{B} , bare branch hydraulic conductance; K_{lb} , leaf blade hydraulic conductance; K_{p} , petiole hydraulic conductance; K_{wb} , whole-branch hydraulic conductance; L_{B} , branch length; Osm, osmolality; PPFD, photosynthetic photon flux density; RH, air relative humidity; T_{a} , air temperature; VPD, water vapour pressure deficit; σ_{sap} , electrical conductivity; Ψ_{s} , soil water potential; Ψ_{s15} , soil water potential measured at depth of 15 cm; Ψ_{s30} , soil water potential measured at depth of 30 cm

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<http://dx.doi.org/10.1016/j.jplph.2017.03.012>

Received 2 January 2017; Received in revised form 21 February 2017; Accepted 21 March 2017

Available online 22 March 2017

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interspecific variation in the ionic effect (Jansen et al., 2011). This variation among vascular plants may reflect also phylogenetic differences in the distribution of lignin and pectins in cell walls (Boyce et al., 2004). Later studies with atomic-force microscope have shown that modulation of hydraulic conductivity is induced by changes in the permeability and thickness of the pit membranes soft gel (pectin) matrix (Lee et al., 2012). Therefore membrane thickness rather than its porosity is the basis for the hydraulic response to changes in ionic content of the xylem sap (Zwieniecki and Secchi, 2012). Other authors (Jansen et al., 2011; Nardini et al., 2011; Santiago et al., 2013) have pointed out electroviscosity as a possible mechanism explaining the ionic effect. Santiago et al. (2013) proposed an electrokinetic flow model to explain the ionic effect according to which electrokinetic effects in the bordered pit membranes are at least partly responsible for this response.

Most of the studies analysing diurnal patterns of plant hydraulic properties are carried out under controlled laboratory conditions (Brodribb and Holbrook, 2004; Bucci et al., 2003; Cordeiro et al., 2009; Johnson et al., 2009; Lo Gullo et al., 2005; Locke and Ort, 2015; Nardini et al., 2005; Voicu and Zwiazek, 2011; Zwieniecki and Holbrook, 1998) and relatively few studies examine daily dynamics of stem, leaf or petiole hydraulic conductance in natural conditions (Brodribb and Holbrook, 2004; Bucci et al., 2003; Johnson et al., 2009, 2011; Öunapuu and Sellin, 2013; Yang et al., 2012). Moreover, most of them are incomplete as regards the time scale because of the lack of nightly measurements. It is known that also ionic content of xylem sap (Nardini et al., 2011; Siebrecht et al., 2003) and pH vary on daily basis (Aubrey et al., 2011; Erda et al., 2014). Xylem sap osmolality – an important characteristic affecting water transport efficiency, pressure gradients and turgor pressure of living cells in plants (López-Portillo et al., 2014) – demonstrates daily dynamics as well (Andersen et al., 1995; Sobrado and Ewe, 2006). However, there is a lack of studies analysing circadian patterns of physio-chemical properties of the xylem sap, especially in terms of plant hydraulic efficiency.

To date there are no studies that consider all these characteristics simultaneously over the course of a day. Therefore we aimed to detect circadian rhythms of physico-chemical properties of xylem sap and branch hydraulic traits in a broadleaved tree growing in field conditions. Although several environmental factors affect plant hydraulic parameters (Brodribb and Holbrook, 2004; Cochard et al., 2000, 2007; Öunapuu and Sellin, 2013; Sellin and Kupper, 2007b), we focussed on the impact of light intensity and air temperature – the most important factors driving circadian patterns in hydraulic properties while excluding effects caused by possible cavitation of xylem conduits. We aimed to ascertain which environmental drivers influence dynamics of the sap properties and whether they are involved in modulation of the plant hydraulic efficiency. First, we hypothesize that plant hydraulic conductance and physico-chemical properties of the xylem sap co-vary diurnally both driven by basic atmospheric conditions. Second, we hypothesize that the enhancement of hydraulic conductivity in response to increasing light intensity in the morning is supported by the upregulation of potassium ion concentration in xylem sap.

2. Materials and methods

2.1. Study area and sample trees

The study site is located at Rõka village (58°14'N, 27°17'E; 40–48 m ASL), eastern Estonia, an area characterised by a northern temperate climate (boreo-nemoral forest zone). Experiments were conducted on hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) saplings growing in the experimental forest plantation at the Free Air Humidity Manipulation (FAHM) site (Kupper et al., 2011). In July and August 2012, we sampled 2 × 112 branches (i.e., two neighbouring branches per tree simultaneously) from 7-yr-old aspen trees growing in the buffer zone of the FAHM site. The branches for every

measurement event were collected from separate trees (112 trees altogether). Mean height (\pm S.E.) of the sample trees was 5.12 ± 0.08 m, the stand density 2500 ha^{-1} .

2.2. Environmental characteristics

The following environmental variables were recorded continuously above the canopy: photosynthetic photon flux density (PPFD) (using LI-190 quantum sensors; Li-Cor Biosciences, Lincoln, NE), air temperature (T_A) and relative humidity (RH) (with HMP45A humidity/temperature probes; Vaisala, Helsinki, Finland). Bulk soil water potential (Ψ_s) was measured with EQ2 equitensiometers (Delta-T Devices, Burwell, UK) at the depths of 15 and 30 cm. The readings of the environmental sensors were stored as average values every 10 min with a DL2e data logger (Delta-T Devices). Atmospheric vapour pressure deficit (VPD) was calculated as the difference between current water vapour pressure and saturated vapour pressure at a given air temperature.

2.3. Hydraulic measurements

Sample branches (mean length \pm S.E. 73 ± 1.5 cm), one branch per tree, were cut from the middle third of the crowns (relative height 0.25–0.60). The cut ends were recut under water and the branches were immediately sampled for hydraulic properties under natural environmental conditions *in situ*. Protection against direct rainfall was provided by a shelter with transparent polycarbonate roof lacking walls. Hydraulic conductance of the whole branch (K_{wb}) and their parts – leaf blades (K_{lb}), petioles (K_p), bare branch (K_B) – was determined at 3-h intervals round-the-clock by the water perfusion method using a high-pressure flow meter (HPFM; Dynamax, Houston, TX), and by removing leaf blades and petioles in sequence. The HPFM was applied in a quasi-steady-state mode. Applying the high pressure method until leaves are infiltrated removes emboli from the vascular system and fills the empty vessels (Nardini et al., 2005), thus their readings indicate plant hydraulic efficiency in water-saturated state. The hydraulic conductance of leaf blades (K_{lb}) was calculated as follows:

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

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

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

During the hydraulic measurements leaf and branch temperatures were recorded using MT2 fast-response temperature probes (Delta-T Devices). The hydraulic characteristics were corrected for the dynamic viscosity of water at 23 °C.

In total 112 branches (8 times a day × 14 daily cycles) were sampled for hydraulic properties, all cut from separate trees. In most cases leaf infiltration and constant readings for the leafy branch were achieved (i.e., leaf blades could be removed) in 20–25 min due to relatively small size of the branches. We concede that dilution of xylem sap is inevitable when using deionised water as a permeation fluid. After completing the hydraulic measurements all leaves were collected and total leaf blade area was determined with a LI-3100C optical area meter (Li-Cor Biosciences, Lincoln, NE).

2.4. Properties of xylem sap

To measure the physico-chemical properties of xylem sap we sampled one branch per tree, choosing a branch located as close as possible to the branch sampled for hydraulic conductance. All leaves were instantly removed from the branch to stop transpiration, the branch was excised from the tree and xylem sap was extracted according to Stark et al. (1985). The sap was extracted from branch segments at a pressure of 2.0 MPa generated by a pressure chamber

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