STOMATAL CONDUCTANCE OF SHORT ROTATION COPPICE BASED ON SAP FLOW MEASUREMENTS AND ITS RESPONSE TO CHOSEN METEOROLOGICAL VARIABLES

STOMATÁLNÍ VODIVOST PLANTÁŽE RYCHLE ROSTOUČÍCH DŘEVIN ODVOZENÁ Z MĚŘENÍ SAP FLOW A JEJÍ OVLIVNĚNÍ VYBRANÝMI METEOROLOGICKÝMI PROMĚNNÝMI

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ABSTRACT

The main aim of this study was to derive stomatal conductance (gs) from sap flow measurements and explore some of possible applications of this method. Sap-flow and other meteorological variables were continuously monitored in poplar-based short rotation coppice (SRC) plantation in Bystřice nad Pernštejnem during growing season 2012. Sap flow of 8 trees was measured using heat dissipation method, then expressed as transpiration per square meter of projection area and by adding into rewritten Penman-Monteith equation the canopy conductance (gs) was obtained. Compared with direct measurements on leaf level this approach is advantageous for obtaining gs, because of integrating all leaf categories of tree or whole canopy. Further analysis also proved, that gs is strongly driven by VPD. Finally, it was found that the relationship between gs and VPD is also influenced by available soil moisture content.

Key words: sap flow, canopy conductance, transpiration, short rotation coppice

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INTRODUCTION

Fast growing forests are broadly defined (Vitousek, 1991) as having average growth rates ranging from 10 to 40 m$^3$/ha/year, with a rotation period shorter than 35–40 years. “Short rotation coppice” (SRC) is one type of fast growing forests systems intended for biomass production on (former) arable land, thus representing an alternative method to food production, especially in those regions where food production is less profitable due to inconvenient climate and/or soil conditions (Trnka et al. 2008). SRC in Europe is usually based on Poplar (Populus spp.) or willow (Salix spp.), grown with dense spacing (up to 10 000 for poplars resp. 20 000 trees/ha for willows). Poplar plantations under climate of Czech Republic usually achieve average biomass increment over 10 m$^3$/ha/year (4.5 t/ha/year of dry matter) and rotation period is typically shorter than 8 years (Havlíčková 2009).

High biomass production and vigorous juvenile growth on one hand demands sufficient and regular water income on the other hand. In the early screening and breeding efforts on energy crops the main focus was on aspects such as potential productivity, disease and frost resistance, coppicing and resprouting ability (Hall & Hanna, 1995; Zsuffa, 1995). However, more recently it has been acknowledged that available water will very often be the most important yield-limiting factor (e.g. Lindroth & Båth, 1999). In last decades SRC plantation based on poplar (Populus spp.) and willow (Salix spp.) are increasingly being grown in Europe as a sustainable source of bioenergy. The largest areas of SRC are situated in Scandinavia (Sweden 12 500 ha) (Dimitriou et al, 2011), Germany, UK, Italy, Belgium and France (Slater et al., 2001). Establishment of new fast growing forests is an effective way to meet the growing demand for wood, therefore reducing the pressure on natural forests (Migliavacca 2008). At the same time, intensively managed ‘‘industrial’’ monospecific forest plantations with a short-rotation period arouse controversy as concerns their benefits for the community, the land and the environment (McKenney et al., 2004). Inadvertent consequences may arise when biomass production is improperly maximized. Competition for water resources may, therefore, become important if energy forests are to cover areas on a regional scale, esp. in semiarid areas. Thus, the evapotranspiration (ET) (as the main loss component of water balance) from energy forests is the key factor determining how the overall water balance will be affected (Grip et al., 1989) and at the same time sets the limits for sustainable growth and development of SRC. ET is referred to as combination of two separate processes whereby water vapour is lost on the one hand from the soil surface by evaporation (E$_s$) and on the other hand from the plant by transpiration (T). The driving force to remove water vapour from the evaporating surface (e.g. leaves) is direct solar radiation, water vapour pressure deficit (VPD) and wind speed. Both evaporation and transpiration occur simultaneously and there is no easy way of distinguishing between the two processes (Allen 1998). Water fluxes in forest ecosystems can be determined by
means of several different approaches: water balance, vapour flux, or sap flow. Water vapour flux measurements over forests (via eddy correlation or Bowen ratio) typically provide average estimates for large areas (ha); the main weakness of these techniques is the inability to determine the exact origin of measured fluxes, since this changes depending on wind direction and wind speed. Sap flow techniques provide information at the individual tree scale (m²). Thus, estimates of stand sap flow are directly dependent on local conditions which may vary over a short distance (Granier et al., 1994). ET can be further described by gradient-diffusion theory with two conductances indicating the major controls of water from the vegetation to the atmosphere. The physiologically based canopy (gc), or (when divided by LAI) stomatal conductance (gs), describes transport from the saturated inner-leaf surface through stomata to the air just outside the leaf. The aerodynamic conductance describes further transport from the air just outside the leaf to the air at a certain reference height above the canopy. The behavior of stomatal conductance (rate of stomata opening/closure) is affected by a number of environmental factors, such as solar radiation, water pressure deficit, temperature, or soil moisture. Thus, the stomatal conductance represents a key parameter that determines energy and water exchanges between canopy and the atmosphere (Wang, 1999). In presented study, the measurements of sap flow were used to calculate stand canopy conductance, by adding it into rewritten Penman-Monteith formula. Calculated stomatal conductance was subsequently linked to the VPD, global radiation and soil moisture.

MATERIALS AND METHODS

Research locality Domanínek is situated near town Bystřice nad Pernštejnem (Czech Republic, Czech-Moravian highland, 49°521'N, 16°235'E, altitude 530 m a.s.l., rain-fed area with mean annual precipitation 587.8 mm, mean annual temperature 6.6 °C). In April 2001, a high density experimental field plantation of poplar clone J-105 (P. nigra x P. maximowiczii) with the total area of 4 ha was established here. The plantation was set up on agricultural land previously seeded predominantly with cereals and potatoes. Hardwood cuttings were planted in a double row design with inter-row distances of 2.5 m and spacing of 0.7 m within rows accommodating density of nearly 10,000 trees/ha. Soil conditions at the location are representative to the wider region with deep luvic cambisol influenced by gleyic processes and with limited amount of stones in the profile. The site itself is situated on a mild slope of 3° with an eastern aspect and is generally subject to cool and relatively wet temperate climate typical for this part of Central Europe with mingling of continental and maritime influences (Trnka et al., 2008). Sap flow of 8 trees was measured during growing season 2012 (2. 6. – 9. 9.), using heat dissipation method (HDP) proposed by Granier (1985) with 20 mm needle sensors (UP GmbH, Cottbus, Germany) used. Trees were chosen in order to express stem diameter variability comprising both dominant and suppressed trees. The measuring element consists of two needle probes (20 mm long and 2 mm in diameter). Each one contains a copper-constantan thermocouple. Those probes are radially inserted in the sapwood of the trunk at distance of approximately 15 cm from each other. The upper probe is
heated at a constant power (0.2 W) and the lower probe is considered as temperature reference. The measurement method relies on the fact, that the sap flow per unit of sapwood area is deducted from the thermal difference between the heated and the reference probe, using an empirical relationship determined in laboratory conditions:

\[ v = 0.199[(\Delta T_{\text{max}}) - 1]^{1.231} \text{ [kg m}^{-2}\text{s}^{-1}] \]

where \( \Delta T \) is the temperature difference between heated and reference probe and \( \Delta T_{\text{max}} \) means the maximum temperature difference representing zero sap flux, usually occurring at nighttime (esp. predawn). In this study the sapwood was assumed to be equal to the whole cross sectional area (CSA) which was determined from the diameter measurements (the thickness of the bark was deducted in order to get the diameter of the xylem) just between heated and reference probe. The CSA value is necessary for relating the calculated sap flow per 1 m\(^2\) of CSA to sap flow of particular tree. Further, taking into account the total CSA (0.11 m\(^2\)) of all stems (n = 160) (measured at 130 cm now including the bark) occupying experimental area (60.76 m\(^2\)) and assuming mean LAI to be 7, the conversion constant 3688.45 (total LAI / total CSA) was developed, allowing derivation of projection area and LAI for each tree from its CSA. Then sap flow could be expressed as transpiration per square meter of foliage. In the next step the rewritten Penman-Monteith equation was used to calculate stand canopy resistance (= r\(_c\), which is inverted value of g\(_s\)).

\[ r_c = \frac{\Delta R_n - G}{\gamma} \frac{\Delta + \gamma}{\lambda ET} + \frac{\rho c_p VPD}{\gamma \lambda ET} \]

where r\(_a\) (s m\(^{-1}\)) is the aerodynamic resistance calculated from wind speed, \( \Delta \) is slope of saturated vapour pressure, \( R_n \) (W/m\(^2\)) represents net radiation (we considered \( R_n \) to be 70 % of global radiation), G (W/m\(^2\)) soil heat flux (G was neglected), \( \gamma \) (0.066 kPa °C\(^{-1}\)) is the psychrometric constant, \( \rho \) (1.23 kg m\(^{-3}\)) is the density of air, \( c_p \) is the specific heat of air (1004 J kg\(^{-1}\) °C\(^{-1}\)) and VPD (kPa) is the water vapour pressure deficit. All variables were calculated using climate data originated from 12 m high mast (measured ca. 2 m above canopy) in the center of the plantation. Wind speed was measured from nearby meteo station at turf grass. Soil moisture was measured using TDR probe (CS616, Campbell Scientific, USA), vertically inserted into the soil in the center of experimental plot, monitoring soil moisture from surface down to 30 cm depth.

**RESULTS AND DISCUSSION**

Highest g\(_s\) values were usually observed between 7:00 and 11:00 each day. Maximum peak g\(_s\) 528.46 mmol/m\(^2\)/s of tree with highest transpiration rate was reached on July 13\(^{th}\), when maximum VPD per this day was only 0.19 kPa. Hinckley et al. (1994) reported maximum g\(_s\) of 480 mmol/m\(^2\)/s, Ceulemans et al. (1989) reported maximum stomatal conductances of about 500 mmol/m\(^2\)/s for five year old trees of the poplar clone Unal (P. trichocarpa x deltoides), in the field. g\(_s\) derived from sap flow integrates all leaves (both sunlit and shaded) and thus usually provides lower values than g\(_s\), measured by porometer, where typically the most active leaves at the upper part of canopy are investigated as e.g. just in Ceulemans et al. (1989) or Hinckley et al. (1994).
Fig. 1 Relationship between $g_s$ and VPD with global radiation below and above 700 W/m$^2$.

After midday $g_s$ starts to decline in response to increasing evaporative demand, which means that stomatal conductance decreases as VPD increases. In Fig. 1 is shown negative relationship between stomatal conductance and VPD for the period June–September 2012. The $g_s$ decreased with an exponential decay function from 171.3 to 0.1 mmol/m$^2$/s for increasing VPD from 0.2 to 4.12 kPa. The 10 minute $g_s$ was strongly driven by VPD. The values in Fig. 1 are divided into two groups according solar radiation level. Red triangles are above and blue circles below 700 W/m$^2$. It was expected that in time with solar radiation above 700 W/m$^2$ the stomata opening are already limited by radiation but may be controlled by VPD. This type of stomatal response to VPD can avoid excessive water loss at high VPD and prevent leaf water potential from falling to a dangerous level, which can be very beneficial during periods of water shortage. Volumetric soil moisture descended from 18% in mid-June to 9% in mid-July and remained this low for the rest of the growing season 2012. In Fig. 2 is shown different stomatal response to VPD in relation to soil moisture content.
Fig. 2 Values of stomatal conductance. Blue circles represent conditions with normal soil moisture (15 – 18 %), and red triangles represent limited soil moisture (9 – 10 %).

Ten minutes values of stomatal conductance processed as natural logarithm are divided into two groups, blue circles represent conditions with normal level of soil moisture (15 – 18 %), and red triangles represent limited soil moisture (9 – 10 %). It can be seen, that in conditions of limited soil water availability closes stomata earlier comparing with higher soil moisture level. Fig. 3 expresses different levels of stomatal behavior between normal and limited soil water treatment in period 2. 6. – 9. 9. 2012. Stomatal conductance of drought stressed poplars was in average by 11.84 % lower compared with normal soil water level. Ceulemans et al. (1988) reported that low soil moisture and soil water potential decreases $g_s$. Also Hall et al. (1998) observed very low conductances coincided with the large soil water deficit. Generally there is a large variation in stomatal response reaction and in seasonal patterns of stomatal activity observed among different poplar clones, which adds to the physiological explanation of the large plasticity of the genus *Populus*. 
Fig. 3 Different levels of stomatal conductance between normal and limited soil water content. Poplars under drought stress shows lower $g_c$ during whole period 2. 6 – 9. 9. 2012.

Further analysis also proved that $g_c / g_s$ can be successfully modeled as a function of global radiation and water pressure deficit (VPD) according Lohammar (Lohammar et al. 1980). Deriving $g_s$ from parameterized Lohammar equation (using only global radiation and VPD), multiplying it by LAI, adding it as $r_c$ (inverted value of $g_c$) into rewritten Penman-Monteith equation and subsequent expressing of sap flow per square meter of projection area can serve as reverse estimation of canopy transpiration under various soil water conditions.

CONCLUSIONS

It was proved, that stomatal conductance of executed poplar plantation moderately responds to soil moisture availability and strongly responds to VPD, which means that in time of higher VPD poplars are able effectively regulate their transpiration by stomata closing. This finding is important because there were found several clones (mainly the productive hybrids of *P. trichocarpa*) for which very pure stomatal control was reported. The stomatal control preventing tree against cavitation and embolism should be taken into account especially when the SRC are established in rain fed areas. This has also very important consequence with respect to climate change when more drought periods are expected. The approach of calculating $g_s$ using Penman-Monteith and Lohammar equations has further application as the core for models estimating transpiration and later balance and last but not least can be helpful during extrapolation and generalization of measured data, gap-filling, etc.
REFERENCES


