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Research paper

Effects of earlywood and latewood on sap flux density-based transpiration estimates in conifers

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ABSTRACT

Heat-based sap flux density (SFD) methods have been widely used to estimate the water use by conifers, but complexities arise due to the heterogeneous nature of conifer sapwood with annual rings of earlywood (EW) and latewood (LW), which differ in water- and heat-conducting properties. Laboratory-based controlled flow experiments using freshly cut stem segments from 11 pine trees were undertaken to evaluate the potential impact of hydraulic architecture of conifer sapwood on tree water use estimates from the Heat Ratio Method (HRM) and Heat Field Deformation (HFD) method, by considering different scenarios regarding the hydraulic conductivity and thermal diffusivity of EW and LW. The results show that the actual water flux was systematically underestimated in Scenario 1 (assuming only EW was water-conductive but thermal diffusivity was mean of EW and LW) and Scenario 3 (assuming equal hydraulic conductivity of LW and EW but thermal diffusivity was that of only EW). However, the mean sap flux densities obtained from 11 sample trees after correction by the LW/EW ratios were pretty close to the gravimetrical flow. Assuming equal hydraulic conductivity of LW and EW and mean thermal diffusivity of EW and LW led to either overestimation or underestimation of water use by individual trees, but the mean tree-scale water use was unbiased when including all this variance in the study system. The observed heterogeneous radial SFD variability from the HFD measurements was closely linked with patterns of successive EW and LW, especially in the central parts of the sapwood where higher SFD values were generally observed. The decreasing SFD patterns towards the cambium and heartwood were partially attributed to the decrease in moisture content, tracheid diameter and the increase in wood density of EW and LW compared with the central sapwood. The results indicated that the LW/EW ratio in stems where sap flow probes have been inserted can be measured a posteriori to correct HRM-based sap flow measurements. The sap flux is recommended to be radially corrected using the SFD patterns from HFD sensors measured at the same location of the HRM measurements in the same tree.

1. Introduction

Conifer forestry is an important industry around the world (Siry et al., 2005). In a number of regions, conifer plantations are located in catchments where forest impact on hydrology has undesirable downstream effects. An understanding of the long-term effects of conifer afforestation on forest hydrology is thus required to guide the sustainable management of potentially impacted water resources. This has generated considerable interest in changes of streamflow (van Wilgen and Richardson, 2012; Perry and Jones, 2017), groundwater recharge (Fan et al., 2014; Ala-Aho et al., 2015) as well as tree water use (Dye et al., 1996; Gyenge et al., 2003; Little et al., 2009; Alvarado-Barrientos et al., 2013; Fan et al., 2016) after forest conversion from native vegetation to conifers.

Various techniques have been developed to estimate forest transpiration and evapotranspiration (Wilson et al., 2001), among which heat-based sap flux density (SFD) methods (e.g. the Heat Ratio Method (HRM) and the Heat Field Deformation (HFD) method) have been widely applied for tree transpiration estimation (Vandegehuchte and Steppe, 2013; Poyatos et al., 2016). The HRM method measures heat pulse velocity from the ratio of the increase in temperature at points downstream and upstream from a line heater probe (Burgess et al., 2001), while the HFD method relates SFD to a temperature difference measured in a changing heat field around a continuously heated needle

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Table 1

Diameter at breast height (DBH), ratio between latewood and earlywood area (LW/EW), sapwood moisture content and dry wood density of 11 stem samples, as well as the type and number of sap flow sensors installed on individual stem samples.

Wood property	Stem sample										
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11
DBH (cm) LW/EW (cm ² cm ⁻²) Moisture content (kg kg ⁻¹) Wood density (kg m ⁻³) Type and number of sap flow sensor installed	17.3 0.65 1.28 0.49 2 HRM 1 HFD	16.7 0.62 1.36 0.46 2 HRM 1 HFD	19.3 0.60 ^a 0.61 ^b 0.64 ^c 1.33 ^a 1.18 ^b 1.21 ^c 0.45 ^a 0.48 ^b 0.50 ^c 2 HRM 3 HFD	21.1 1.55 1.16 0.53 2 HRM 1 HFD	20.5 0.94 1.27 0.52 2 HRM 1 HFD	18.0 0.46 1.41 0.49 2 HRM 1 HFD	17.2 0.47 1.47 0.45 2 HRM 1 HFD	19.8 0.77 1.53 0.44 2 HRM	18.4 0.35 1.32 0.54 2 HRM	17.5 0.51 1.56 0.46 2 HRM	21.3 0.80 1.38 0.53 2 HRM

Note: a, b, c represent wood properties measured on northern, southwestern and southeastern sides of Sample 3, respectively.

(Nadezhdina et al., 2012). However, previous research has shown that estimating conifer water use from heat-based sap flow measurements is challenging due to a number of sources of uncertainty, e.g. inaccuracy in determining conducting sapwood area, difficulty in establishing zeroflow due to night-time transpiration, and probe-induced effects of wounding (Nadezhdina et al., 2002). A major source of uncertainty is the spatial variations in SFD with depth into the sapwood in different circumferential directions, which are largely dependent on wood types (e.g. coniferous, diffuse-porous and ring-porous trees) (Berdanier et al., 2016), as well as changing environmental factors such as the variability of soil water availability and evaporative demand (Dragoni et al., 2009).

The sapwood structure of conifers consists of alternate earlywood (EW) and latewood (LW) tissues, which induces differences in hydraulic and thermal properties (Domec and Gartner, 2002) and thus makes single-point SFD measurements by these heat-based SFD methods difficult. Several hydraulic conductivity studies on conifers have found EW to be the only conductor of water (Harris, 1961; Booker and Kininmonth, 1978; Whitehead and Jarvis, 1981), but Domec and Gartner (2002) found the hydraulic conductivity of EW to be 11 times higher than that of LW in Douglas-fir (Pseudostuga menziesii (Mirb.) Franco). The thermal diffusivity can be also different between EW and LW due to their differences in wood moisture content and dry wood density. The measurement points (e.g. thermocouples) of the HRM and HFD sensors can be located in either EW or LW after installation in the sapwood. However, to our knowledge no studies have distinguished the differences in hydraulic conductivity and thermal diffusivity between EW and LW when estimating conifer transpiration using the HRM and HFD methods (Kurpius et al., 2003; Ford et al., 2004; Gartner et al., 2009; Guyot et al., 2015).

Upscaling radial SFD measurements by heat-based sap flow sensors to tree-scale transpiration has been widely studied (Jiménez et al., 2000; Nadezhdina et al., 2012; Guyot et al., 2015), but the resin exudation issue arose when validating the accuracy of these sensors against the known values of actual transpiration in the field (Dye et al., 1996; Alvarado-Barrientos et al., 2013). Dye et al. (1996) evaluated the accuracy of SFD measurements in pine trees (Pinus paluta Schldl. Et Cham.) using an in-situ validation approach, where cut trees were suspended in a water reservoir to enable monitoring of transpiration through water uptake. It was found that continuous resin exudation from wounding during the field experiments had a significant effect on SFD measurements. Alvarado-Barrientos et al. (2013) used a similar insitu approach to evaluate a radial SFD profile model based on HRM measurements. Both Dye et al. (1996) and Alvarado-Barrientos et al. (2013) observed noticeable scatters in their results when comparing measured sap flow with actual flow. In-situ validation of SFD using a water uptake approach in conifers will undoubtedly be affected by the resin exudation and will result in imprecision for validating SFD measurements.

To alleviate the *in-situ* issue of resin exudation and control the velocity of water being generated and the thermal conditions, controlled flow experiments were implemented in the laboratory using freshly cut stem segments following Steppe et al. (2010). SFD measurements were performed by using a combination of HRM and HFD sensors, the former being chosen for its acceptable accuracy of 0.5 cm h⁻¹ (Burgess and Downey, 2014), and the latter for enabling multi-point measurements along the radial profile from the cambium to the heartwood. This study mainly investigated the effects of earlywood and latewood on tree water use in conifers from discrete SFD point measurements. Specific objectives were to: (i) verify the accuracy of heat-based SFD measurements from controlled gravimetric flow rates; (ii) investigate the detailed radial SFD profiles across all EW and LW tissues in the sapwood by the sequential HFD sensor approach; (iii) and test the effects of EW and LW on SFD estimates by considering different scenarios regarding their hydraulic conductivity and thermal diffusivity.

2. Material and methods

2.1. Tree stem samples

Controlled flow experiments were conducted in the Civil Engineering laboratories at The University of Queensland, Australia. Over a one-month period, a total of 11 coniferous trees (*Pinus elliottii* Engelm var. elliottii \times *Pinus caribaea* Morelet var. hondurensis) were harvested from an 11-year-old pine plantation forest located in a subtropical climate on Bribie Island, South-East Queensland (SEQ), Australia (26°59′04′S, 153°08′16′E). Stem samples of ~50 cm taken at breast height with an average diameter of 18.9 ± 1.5 cm (Table 1) were cut three days before each experiment, and brought back to the laboratory in black plastic bags filled with water to avoid dehydration. In the laboratory, stem segments of ~30 cm were re-cut under water to prevent the occurrence of embolisms and prepared just before the beginning of each experiment.

2.2. Gravimetric flow system

To test the accuracy of the two commonly used methods for measuring sap flux density (HRM and HFD), a gravimetric flow system was built using cut stem segments in which the sap flow sensors were installed simultaneously (Fig. 1) following Steppe et al. (2010). Flow rates of water were maintained constant using a constant head overflow system. The system consisted of a container filled with tap water and placed on a trolley jack, which included a smaller internal overflow container. The small internal container was connected to a cylindrical reservoir constructed for each individual stem segment through a water-filled siphon. The pressure head in the water reservoir was adjusted by changing the height of the trolley. A very small head difference from internal container to outer container was maintained manually to avoid aeration of the water. Water flow rates through the stem segments were obtained using an electronic balance (MVL20000, OHAUS, Victoria, Australia) by measuring the change in mass at 20 s intervals. Gravimetric flux densities were obtained by dividing the flow

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