Agricultural and Forest Meteorology 249 (2018) 264–274

Contents lists available at ScienceDirect
Agricultural and Forest Meteorology
journal homepage: www.elsevier.com/locate/agrformet

Research paper

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

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A R T I C L E I N F O

Keywords:
Sap flux density
Radial profile
Hydraulic conductivity
Thermal diffusivity
Upscaling

A B S T R A C T

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 flux 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., 2013), while the HFD method relates SFD to a temperature field around a continuously heated needle.
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.

<table>
<thead>
<tr>
<th>Wood property</th>
<th>Stem sample</th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
<th>S4</th>
<th>S5</th>
<th>S6</th>
<th>S7</th>
<th>S8</th>
<th>S9</th>
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<tbody>
<tr>
<td>DBH (cm)</td>
<td></td>
<td>17.3</td>
<td>16.7</td>
<td>19.3</td>
<td>21.1</td>
<td>20.5</td>
<td>18.0</td>
<td>17.2</td>
<td>19.8</td>
<td>18.4</td>
<td>17.5</td>
<td>21.3</td>
</tr>
<tr>
<td>LW/EW (cm² cm⁻²)</td>
<td></td>
<td>0.65</td>
<td>0.62</td>
<td>0.60*</td>
<td>0.61*</td>
<td>0.64*</td>
<td>1.55</td>
<td>0.94</td>
<td>0.46</td>
<td>0.47</td>
<td>0.77</td>
<td>0.35</td>
</tr>
<tr>
<td>Moisture content (kg kg⁻¹)</td>
<td></td>
<td>1.28</td>
<td>1.36</td>
<td>1.33*</td>
<td>1.32*</td>
<td>1.21</td>
<td>1.16</td>
<td>1.27</td>
<td>1.41</td>
<td>1.47</td>
<td>1.53</td>
<td>1.32</td>
</tr>
<tr>
<td>Wood density (kg m⁻³)</td>
<td></td>
<td>0.49</td>
<td>0.46</td>
<td>0.45*</td>
<td>0.48*</td>
<td>0.50*</td>
<td>0.53</td>
<td>0.52</td>
<td>0.49</td>
<td>0.45</td>
<td>0.44</td>
<td>0.54</td>
</tr>
<tr>
<td>Type and number of sap flow sensor installed</td>
<td></td>
<td>2 HRM 1</td>
<td>2 HRM 1</td>
<td>2 HRM 3 HFD</td>
<td>2 HRM 1</td>
<td>2 HRM 1</td>
<td>2 HRM 1</td>
<td>2 HRM 1</td>
<td>2 HRM 1</td>
<td>2 HRM 1</td>
<td>2 HRM 2 HRM</td>
<td></td>
</tr>
</tbody>
</table>

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 zero-flow 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 (Pseudotsuga menziesii (Mirb.) Franco). The thermal diffusivity can also be 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; Goyet et al., 2015).

Upscaling radial SFD measurements by heat-based sap flow sensors to tree-scale transpiration has been widely studied (Jiménez et al., 2014; Nadezhdina et al., 2012; Goyet 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 palustris Schidl. 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 in-situ 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 scatter 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 × 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
rates with the active sapwood area. The water flux density varied between 5 and 80 cm$^3$ cm$^{-2}$ h$^{-1}$ at constant water heads varying between 0.01–0.40 m, similar to that observed by Steppe et al. (2010). Each constant head of water was maintained for a minimum of 30 min. The sap flux densities measured by heat-based sensors were then compared with flux density measurements obtained gravimetrically.

### 2.3. Absolute SFD measurements with the Heat Ratio Method

The commercially available HRM sensors (SFM1, ICT International Pty Ltd, Armidale, Australia) were used in the controlled flow experiments to estimate absolute values of SFD. Two HRM sensors per stem sample were used as a common practice in sap flow studies in view of costs and effort involved. HRM sensors consist of a line heater probe with two point temperature probe vertically aligned 5 mm above and below. Each temperature probe has a thermistor located at 12.5 mm and 27.5 mm from the base of the probe, respectively. Based on the measurements of temperature increase from the initial temperature, the heat pulse velocity is calculated from Equation (3) and (4) (Burgess et al., 2001; Steppe et al., 2010).

\[
\frac{c}{\rho_f} = \frac{\rho_f c_f}{\rho_d c_w} \left( \frac{m_c - m_{c,FSP}}{\rho_w} \right)
\]

(3)

\[
F_{v,FSP} = 1 - G \left( \frac{\rho_w}{\rho_d} + m_{c,FSP} \right)
\]

(6)

where $m_c$, $\rho_w$, and $\rho_d$ are the fresh weight and oven-dried weight of wood sample (kg), and $c_w$ and $c_d$ is the specific heat capacity of water (4186 J kg$^{-1}$ K$^{-1}$) and dry wood (1200 J kg$^{-1}$ K$^{-1}$) at 20 °C, respectively.

The thermal conductivity is estimated from Vandegehuchte and Steppe (2012a) taking into account both bound and unbound water:

\[
K = K_w (m_c - m_{c,FSP}) \frac{\rho_d}{\rho_w} + 0.04186 (21.0 - 20.0 F_{v,FSP})
\]

(4)

where $K_w$ is the thermal conductivity of water at 20 °C (0.5984 W m$^{-1}$ K$^{-1}$), $m_c$ is the sapwood moisture content (moisture per dry weight, kg kg$^{-1}$), and $m_{c,FSP}$ is the wood moisture content at fiber saturation point, $F_{v,FSP}$ is the void fraction of wood at fiber saturation point, $\rho_w$ and $\rho_d$ are the density of water (1000 kg m$^{-3}$) and dry wood (kg m$^{-3}$), respectively. The wood moisture content at fiber saturation point can be determined according to Roderick and Berry (2001):

\[
m_{c,FSP} = 0.2 (\rho_d \rho_w^{-1})^{-1/3}
\]

(5)

The void fraction at fiber saturation point can be determined from as:

\[
F_{v,FSP} = 1 - G \left( \frac{\rho_w}{\rho_d} + m_{c,FSP} \right)
\]

(6)

where G is the specific gravity of wood (dry mass per fresh volume divided by density of water) at moisture content $m_c$, $\rho_{cw}$ is the cell wall density (1530 kg m$^{-3}$) (Kollmann and Côté, 1968).

Installing probes in the sapwood will create a local wounding effect around damaged xylem. A natural wounding effect observed in living conifer trees was not observed in the cut stem segments. Thus, the wound width was estimated based on the mechanical damage from the probe installation. Burgess et al. (2001) created a numerical model that gives wounding correction coefficients based on the size of the drilled probe hole. To perform the wounding correction of heat pulse velocity
measurements, equation (7) is used:
\[
V_c = bV_h + cV_d + dV_w
\]
(7)

where \(V_c\) is the corrected heat pulse velocity, \(b\), \(c\) and \(d\) are wounding correction coefficients (1.6821, −0.0015 and 0.0002 based on the determined wound width of 1.7 mm, respectively). Sap flux densities from HRM measurements were then estimated as:
\[
SFD_{HRM} = \frac{V_c (c_d + m_s c_w)}{\rho_s c_w}
\]
(8)

Even with careful installation of heater and temperature probes, a small degree of misalignment will always be present. To correct this, zero flow conditions were maintained for at least one hour and the average \(Q_{HRM}\) offset for each sensor was added or subtracted from SFD measurements to account for probe misalignment (Steppe et al., 2010).

2.4. Radial profile correction with the Heat Field Deformation method

The commercially available HFD sensors (HFD8-100, ICT International Pty Ltd, Armidale, Australia) were used to estimate the radial SFD profiles. A detailed description of the HFD sensors can be found in Nadezhdina et al. (2002). Each temperature probe consists of eight thermocouples evenly spaced (i.e. 10 mm) with the first measurement point at 20 mm. SFD at each measurement point can be determined as (Nadezhdina et al., 1998; Nadezhdina et al., 2012; Vandegehuchte and Steppe, 2012b):
\[
SFD_{HFD} = 3600D (K_0 + dT_{sym} - dT_{asy} - Z_w) Z_s L_w
\]
(9)

where \(dT_{sym}\) is the temperature difference between symmetrical positioned thermocouples, \(dT_{asy}\) is the temperature difference between asymmetrical thermocouples, \(Z_w\) is the distance between heater and upper axial thermocouple (i.e 15 mm), \(Z_s\) is the distance between the heater and tangential thermocouple (i.e 5 mm), \(L_w\) is the sapwood depth and \(K_0\) is the absolute value of \(dT_{sym}-dT_{asy}\) under conditions of zero sap flow (Fig. 1).

2.5. Hydraulic conductivity and thermal diffusivity scenarios

To test the effects of EW and LW contributions to water flow in the studied conifer hybrid, it has been decided to base results on: (1) a scenario (SC1) that assumed only EW was water-conductive but thermal diffusivity was mean of EW and LW; (2) a second scenario (SC2) where EW and LW were equally water-conductive and thermal diffusivity was mean of EW and LW; and a third scenario (SC3) where EW and LW were equally water-conductive but thermal diffusivity was that of EW. A fourth scenario (SC4) based on the finding of Domec and Gartner (2002), an 11 fold difference in hydraulic conductivity of EW and LW with mean thermal diffusivity of EW and LW was considered. However, assuming Darcy’s Law and flow in porous media to be representative of flow in conifers, the known difference in hydraulic conductivity between EW and LW, and the EW area ratio of 0.63 and LW area ratio of 0.37 to total sapwood area, the water flow in the LW was found to be 5.1% of that in the EW, therefore supporting the use of only SC1, SC2 and SC3, as SC4 would be similar to SC2. These scenarios provided different sap flow outputs, which were compared with the actual gravimetric values. The mean absolute errors (MAE) were calculated to evaluate the performance of different hydraulic conductivity and thermal diffusivity scenarios.

2.6. Experimental protocol

All experiments were undertaken at a constant room temperature of 25 °C and a relative humidity of approximately 70%. Prior to each experiment, a 0.01–0.02 m thick disc was cut off from both ends of the stem segments 3–4 times over a period of 1–2 days to remove resin from the sample ends. This could avoid further resin exudation and thus flow blockage when running the experiments. Stem samples were continuously kept moist and cool during the handling and storage. On the day of testing, each individual stem sample was trimmed to be 0.3 m long using a combination of a sharp chain saw and single edge razor-blade. After trimming, a 0.05 m strip of bark and cambium was removed from the bottom of the sample to enable attachment of the cylindrical reservoir. Two HRM sensors were placed at in-situ breast height on natural northern and southern sides of all 11 stem samples, while the HFD sensor was installed in the northern position 0.1 m upstream of the HRM sensor on Samples 1–7 for radial profile correction (Fig. 1). HRM sensors were installed to measure SFD at 10 and 25 mm depths below the cambium, whereas HFD sensors were used to measure SFD at 10, 20, 30, 40, 60, 70 and 80 mm depths below the cambium. Following the installation of sensors, the stem samples were suspended in the gravimetric flow system and flushed for 30–60 min before commencing the experiment. HRM sensors were set up to log at 3 min intervals, while HFD sensors logged every 2 min. The difference in logging interval was due to the software limitation. Each experiment was run for at least 30 min and yielded a minimum of 10 measurements per sensor per flow rate. At the end of each experiment, the zero flow condition was maintained for 1 h to correct probe misalignment for HRM. Initial tests had been conducted to estimate the time required to obtain zero flow conditions. Sample 3 was further used to determine the circumferential variability of SFD by rotating an HFD sensor counter-clockwise between the north, southwest and southeast directions. The water head in the stem reservoir varied between 0.005 m, 0.05 m and 0.2 m. Sample 3 was also used to investigate the detailed radial profile pattern of SFD using a HFD sequential sensor approach by moving the sensor partially at 2 mm increments across the radial profile in the northern and southwestern positions at a constant water head of 0.1 m. Following the procedure of Vandegehuchte and Steppe (2012a), a piece of sapwood sample along the HFD sensors (∼50 mm long) was taken after finishing each experiment. Those samples were weighed and dried at 60 °C until all moisture had evaporated. The dried samples were afterwards weighed and their volume was determined using Archimedes’ principle. Moisture content and wood density of the entire sapwood were determined for individual stem samples. But for Sample 4, owing to its larger ring widths, moisture content and wood density were measured separately for EW and LW tissues. Mean moisture content and wood density of EW and LW were used to obtain wood characteristics needed for Scenarios 1 and 2 (thermal diffusivity being mean of EW and EW), while moisture content and wood density of EW and LW determined from Sample 4 were used in SFD calculations for Scenario 3 (thermal diffusivity being that of EW).

2.7. Sapwood analysis

The conducting sapwood area was determined from dye tracer infiltration of Toluidine Blue (e.g., McMannet et al., 2007) followed by visual observations. Earlywood and latewood were distinguished visually (Guyot et al., 2015) by their distinct colour patterns (dark for LW and white for EW), and the radial boundaries of EW and LW were measured for each stem sample using a high precision calliper (i.e. ± 0.01 mm, electronic digital, J.B.S.). A microscopic analysis was conducted using an Olympus SZH10 microscope (Tokyo, Japan) in combination with Image Pro Plus version 5.0 (MediaCybernetics, Maryland, USA) to determine the sapwood tracheid size and density across the radial profile. Six consecutive EW and LW samples were measured starting from the cambium towards the heartwood for a tree stem following the same procedure of Mencuccini et al. (1997). For each EW and LW sample, 200 tracheids were used and the tracheid diameter and tracheid density were measured.
3. Results

3.1. Differences in wood properties between EW and LW

The average EW area and LW area from 11 stem samples accounted for 63% and 37% of the total sapwood area, respectively. This resulted in an average area ratio between LW and EW of 0.66 ± 0.32 (cm² cm⁻²), where Sample 5 and especially Sample 2 exhibited a much higher LW/EW area ratio (0.94 and 1.55 cm² cm⁻², respectively) as compared to the other stem samples (Table 1). The mean moisture content and wood density from 11 stem samples were found to be 1.38 ± 0.11 (kg kg⁻¹) and 0.49 ± 0.05 (kg m⁻³), respectively. Further analyses from Sample 4 revealed clear differences in wood properties between EW and LW (Table 2). The average moisture content was 2.49 ± 0.16 (kg kg⁻¹) for EW and 0.85 ± 0.12 (kg kg⁻¹) for LW. Differences were also found for dry wood density, with 0.29 ± 0.01 (kg m⁻³) and 0.61 ± 0.09 (kg m⁻³) for EW and LW, respectively. The average tracheid diameter (and density) was 42 ± 2 μm (505 ± 35 tracheids mm⁻²) for EW and 23 ± 5 μm (576 ± 15 tracheids mm⁻²) for LW. Generally, the central sapwood exhibited higher moisture content and tracheid diameter, but lower wood density and tracheid density compared with the outer and inner sapwood.

3.2. Whole-tree water use based on HRM measurements

Estimates of SFD using two radial measurement points per HRM sensor without radial profile correction shows a clear difference among three scenarios when compared with gravimetric flux density (Fig. 2). For SC1, the majority of SFD estimates were below the 1:1 regression line, indicating that SFD measurements with two HRM sensors per tree underestimate the actual water flux (on average 39% underestimation), especially at higher sap flux densities. Samples 5 and 4, with high LW/EW ratios, exhibited much lower sap flux densities as compared to the other stem samples. However, the SFD estimates were closely scattered around the 1:1 regression line in SC2, resulting in generally lower MAE as compared to SC1 (Table 3). The whole-tree water use was either overestimated or underestimated by assuming EW and LW were equally water-conductive, but the mean tree water use estimated from the 11 tree samples was close to the actual water flux (Fig. 2). The SFD of most trees were underestimated in SC3, ranging from 7% to 39%, but resulting in similar MAE as compared to SC2. The difference in the standard deviation as shown in Fig. 2 for each sample was primarily a result of differences between the northern and southern HRM measurements. The standard deviation for each measurement point increased with increasing water flow rates, but did not exceed the standard deviation between measurement points.

The linear regression slopes between HRM-measured SFD (SFD₁) and gravimetric flux density (SFD₂) for individual trees under different scenarios were presented in Table 4. Generally, the mean SFD₁/SFD₂ values decreased with increasing EW/LW ratios. We found significantly negative power relationships between SFD₁/SFD₂ and LW/EW ratio (Table 4). The power fit functions were further tested to correct the sap flow measurements from HRM sensors with the determined LW/EW ratio of individual trees (Fig. 3). As seen from Fig. 3, the corrected SFD estimates were closely scattered around the 1:1 regression line, and the mean sap flux density obtained from 11 sample trees after correction with LE/EW ratios were pretty close to the actual values under three scenarios. Comparing Figs. 2 and 3, it is easy to see that the LW/EW ratio in the stems where sap flow probes have been inserted can be measured a posteriori to correct sap flow measurements from HRM sensors.

3.3. Radial profile correction of single-point HRM measurements

To investigate the SFD profiles in deeper sapwood not captured by HRM sensors, a radial profile correction of the 7 selected stem samples was further conducted based on supplementary HFD measurements. Radial profile correction of averaged HRM measurements at 10 mm using the average of radial SFD from HF measurements under three scenarios is shown in Fig. 4. It was difficult to observe SFD far below 20 cm² cm⁻² h⁻¹ for the 7 stem samples selected due to their high hydraulic conductivities. The results show that SFD estimates for most stem samples in SC1 underestimated gravimetric flux densities, which became more obvious after radial correction. In contrast, the majority of SFD estimates in SC2 were closely scattered around the 1:1 regression line, whereas the estimated values were moving towards overestimation of gravimetric flux density after radial correction. The SFD estimates in SC3 were distributed closer to the 1:1 regression line, but the SFD was slightly overestimated or underestimated after radial correction. For SC1, radial profile corrections reduced the MAE from gravimetric flux densities for Samples 2 and 3, but resulted in no improvement in MAE for Sample 6, or decreased the accuracy for Samples 1, 4, 5 and 7 (Table 1). No obvious improvement in MAE was achieved for any stem samples in SC2 and SC3 after radial correction.

To help understand the causes of the discrepancy between the sap flux density and gravimetric flux density after radial profile corrections, the radial SFD profile variability for Samples 1–7 and the EW and LW pattern for all 11 stem samples were presented in Fig. 5. As we can see, the radial SFD profiles and EW/LW patterns differed significantly among stem samples. The radial SFD profile of Sample 2, with reduced mean absolute errors in SFD after the radial correction in SC1, displayed an asymmetric pattern skewed to the outermost sapwood, while Sample 5, with increased mean absolute errors in SFD after the radial correction, showed relatively small peaks in SFD over the radial profile. The much higher SFD values in the outer sapwood for Sample 2 yielded a radially-averaged SFD value that was higher than the single-point SFD value from the HRM measurement, which thus caused a reduction in mean absolute errors. However, the small changes in SFD over the radial profile for Sample 5 resulted in a slightly lower radially-averaged SFD value compared with the single-point SFD value, thereby increasing the mean absolute errors in SFD after the radial correction.

3.4. Effects of EW and LW on radial SFD measurements

Sample 3 was further tested for the effects of sapwood heterogeneity on SFD measurements (Fig. 6). The northern position showed an asymmetric pattern skewed to the deeper sapwood, whereas southeast...
and southwest positions exhibited a more monotonic pattern. The majority of SFD measurement points for southeastern and southwestern positions were found to be located in the LW as compared to the northern position, where higher SFD values were observed in the EW. The southwest and southeast probes showed lower SFD values compared with the north sensor, which can be partially attributed to the reduced sapwood moisture content and increased dry wood density on the southwestern and southeastern sides of trees (Table 2). The northern position was used to radially correct Sample 3, hence reducing MAE after radial correction, but the use of southwestern or southeastern probes would have resulted in a noticeably different MAE based on the difference in SFD between the positions.

**Table 3**
Mean absolute error (MAE) from the 1:1 regression line for two-point HRM (MAE_{HRM}), one-point HRM without radial correction (MAE_{enc}) and one-point HRM with radial correction (MAE_{ec}) under three hydraulic and thermal scenarios. Changes in MAE (ΔMAE) are given for single-point HRM before and after radial correction.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Scenario 1</th>
<th>Scenario 2</th>
<th>Scenario 3</th>
</tr>
</thead>
<tbody>
<tr>
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<td>MAE_{enc}</td>
<td>MAE_{ec}</td>
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<tr>
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<td>1.4</td>
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<tr>
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<td>17.8</td>
<td>5.9</td>
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<tr>
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<tr>
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<tr>
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<td>8.4</td>
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<td>6.7</td>
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<tr>
<td>11</td>
<td>15.3</td>
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</table>
Results in Figs. 5 and 6 indicate that the positioning of measurement points in LW may have an effect on radial SFD profile shape and subsequently the radial correction. A 2-mm incremental radial profile was further created for the northern and southwestern positions in Sample 3 using the sequential HFD sensor approach to test if the observed difference in radial profile shapes resulted from the sensor positioning (Fig. 7). Generally, measurement points located in the LW tissues showed a trend of reduced SFD values compared with adjacent values observed in the EW tissue for both northern and southwestern positions, with the highest peaks of SFD located in the EW. Towards to the bark (below 20 mm), where the EW width decreased and became similar to that of LW, few variations in SFD were detected and SFD tended to increase regardless of the measurement points being in contact with EW or LW. Close to the heartwood (beyond 50 mm), SFD showed a decreasing trend still with generally lower SFD values in the LW compared with neighboring values in the EW. Unfortunately, the sequential sensor profile was undertaken at 0.1 m pressure head and thus not directly comparable to that in Fig. 6. However, it is evident that the static and sequential sensor profile shapes for the northern and southwestern positions generally exhibited similar patterns, although variations in

<table>
<thead>
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<th>Stem sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>LW/EW (cm² cm⁻²)</td>
<td>S1  S2  S3  S4  S5  S6  S7  S8  S9  S10  S11</td>
</tr>
<tr>
<td>Slope of linear regression</td>
<td>SC1  0.65  0.62  0.60  1.55  0.94  0.46  0.47  0.77  0.35  0.51  0.80</td>
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<tr>
<td></td>
<td>SC2  1.06  0.94  0.84  0.56  0.78  1.24  1.34  0.67  0.78  1.24  1.34</td>
</tr>
<tr>
<td></td>
<td>SC3  0.92  0.79  0.75  0.61  0.69  0.92  0.93  0.78  0.87  0.84  0.76</td>
</tr>
<tr>
<td>Power fit function of SFD¹ /SFD² and LW/EW</td>
<td>SC1 SFD¹/SFD² = 0.377(LW/EW)⁻⁰.⁸⁸⁷ R² = 0.883</td>
</tr>
<tr>
<td></td>
<td>SC2 SFD¹/SFD² = 0.708(LW/EW)⁻⁰.⁵⁶⁴ R² = 0.731</td>
</tr>
<tr>
<td></td>
<td>SC3 SFD¹/SFD² = 0.701(LW/EW)⁻⁰.²⁸⁰ R² = 0.757</td>
</tr>
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</table>

Fig. 3. Relationship between gravimetric flux density and two-point HRM-based sap flux density corrected by the ratio of LW and EW for each of the 7 stem samples under three scenarios. SC1 assumes only EW is water-conductive but thermal diffusivity is mean of EW and LW, SC2 EW and LW equally water-conductive and thermal diffusivity mean of EW and LW, SC3 EW and LW equally water-conductive but thermal diffusivity that of EW. The dashed line shows the 1:1 regression line. The vertical error bars represent standard deviation for sap flux density.
SFD between EW and LW were not captured by the static HFD sensor. Circumferential variations in radial SFD profiles were difficult to evaluate based on Fig. 6 as a result of measurement point locations, but the sequential sensor profiles (Fig. 7) did show obvious variations between the northern and southwestern positions.

4. Discussion

4.1. Effective sapwood area to be considered influences whole-tree water use upscaling

The sapwood-heartwood boundary determined by the dye infiltration method corresponded well with the radial SFD measurements. Within the sapwood area, the dye infiltration showed preferential flow in EW, but water flow was also observed in LW. This was further supported by the detection of positive sap flux density in LW measured by HFD sensors, which is similar to what Dye et al. (1991) found for *Pinus patula* but different from the zero LW conductivity experienced in other studies (Harris, 1961; Booker and Kininmonth, 1978; Whitehead and Jarvis, 1981). The lower SFD values observed in LW can be a result of hydraulic architecture. The observed average conduit diameter of 42 μm and conduit density of 505 conduits mm\(^{-2}\) for EW as well as corresponding values of 23 μm and 76 conduits mm\(^{-2}\) for LW in this study were similar to what Domec and Gartner (2002) observed for Douglas-fir. The EW/LW ratio of ~2 in average conduit diameter and the small difference in conduit density supported EW as being the primary conductor of sap flow, but could also explain the presence of sap flow being detected in LW, indicating that sap flow in LW has also to be considered when estimating whole-tree water use of conifers using the HRM and HFD methods. Yet, it still remains difficult to evaluate the damage to tracheids caused when preparing the stem samples for each experiment.

The actual water flux of the 11 stem samples were mostly underestimated if the conductivity of LW was not considered, resulting in an average systematic underestimation of 39%. Sample 5 and especially Sample 4 exhibited a much higher LW/EW area ratio compared with the other stem samples, which may explain the clear underestimation of gravimetric flux density in SC1 (up to 76%). This confirms that the relative proportion of LW has to be taken into account when upscaling discrete measurement of sap flux density to whole-tree water use. The actual water flux of individual trees may be overestimated or underestimated depending on the positioning of sap flow sensors by considering the same hydraulic conductivity of EW and LW, but a set of estimates can give a mean close to the actual value. This is because tree-to-tree variations in EW and LW areas can be minimized by taking larger tree samples as the radial SFD variability associated with the positioning of HFD measurement points in contact with EW or LW tissues tends to be random. Despite the great contributions of EW and LW properties to the difference between sap flow measurements and the gravimetric flow, other assumptions and constants used for the HRM calculations may also affect the sap flow outputs, e.g., the errors arising from inaccurate probe spacing (Green et al., 2003), the wounding

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**Fig. 4.** Relationship between gravimetric flux density and one-point HRM-based sap flux density without and with radial correction by HFD sensors for each of the 7 stem samples under three scenarios. SC1 assumes only EW is water-conductive but thermal diffusivity is mean of EW and LW, SC2 EW and LW equally water-conductive and thermal diffusivity mean of EW and LW, SC3 EW and LW equally water-conductive but thermal diffusivity that of EW. NC indicates that one-point HRM measurements are not radially corrected by radial SFD measurements, and C indicates that one-point HRM measurements are radially corrected. The dashed line shows the 1:1 regression line. The vertical error bars represent standard deviation for sap flux density.
correction coefficients b, c and d (1.6821, −0.0015 and 0.0002) empirically obtained from the measured wound width of 1.7 mm (Burgess et al., 2001), and the assumed constant specific heat capacity of water and dry wood within and between trees (Bouguerra, 2001).

4.2. Radial SFD variability is impacted by coniferous earlywood and latewood tissues in tree rings

The radial SFD profile of Sample 2 displayed an asymmetric pattern skewed to the outer sapwood, which was also observed by Cohen et al. (2008) for Pinus halepensis Mill. The relatively small peak in the central sapwood of Sample 5 was similar to the SFD pattern found by Dye et al. (1991) in Pinus paluta Schldl. Et Cham. These radial SFD distributions were consistent with most common patterns of radial sap flux density form a Gaussian bell, exhibiting a peak between sapwood depths of 10 and 30 mm (Nadezhdina et al., 2002; Cohen et al., 2008), a decreasing pattern towards the heartwood (Dye et al., 1991; Ford et al., 2004). The general decreasing trend in sapwood moisture content and tracheid diameter but increasing trend in dry wood density of EW and LW towards the outer and inner sapwood (Table 2) can partially explain the decreasing sap flux density below ~20 mm depth and beyond ~50 mm depth. The embolisms- and tyloses-based inactivation of xylem and the resulted decrease in vessel diameter with depth towards the heartwood may have also contributed to the decreasing SFD in older parts of the sapwood (beyond 50 mm) (Tyree and Zimmermann, 2002; Cohen et al., 2008). Compared with the SFD values at the outermost sapwood, a higher SFD was found to be present in the central part of sapwood beyond the maximum measurement depth of HRM (i.e., 25 mm), which suggests that the low MAEHRM (Table 3) in SC2 does not necessarily reflect the large SFD variability over the radial profile. This was supported by the general overestimation of the gravimetric flux density from the sap flow approach for SC2 after radial profile correction (Fig. 3). Furthermore, the low MAEHRM in SC2 was expected to be a result of the increased sapwood area compared with that in SC1 where only the earlywood was assumed to be water-conductive, compensating for the missed larger radial SFD values in deeper sapwood. The underestimation of gravimetric flux density in SC1 (Fig. 2) can be partially explained by the lack of radial correction, since only part of stem samples in SC1 have achieved a low MAE after radial correction.

A majority of radial SFD measurement points was found to be located in LW tissues (Figs. 5 and 6). This could explain the discrepancy in the results after the radial profile correction. These findings were further confirmed by the sequential sensor profiles (Fig. 7), which exhibited lower SFD values in LW between 20 mm to 50 mm depths compared to that measured in the adjacent EW. The measurement points (thermocouples) on the HFD sensors are spaced 10 mm apart, but their footprint size (influencing depth) may vary from a few mm to up to 10 mm, most likely depending on the energy input from the heater needle, the sap flow rates and the wood properties (hydraulic conductivity and thermal diffusivity). The small variations in SFD found towards the bark are likely a result of the decrease in thickness of the EW and LW tissues. With reduced thickness, SFD is expected to be
affected by the boundary conditions created from the close proximity of the EW and LW tissues. That is, SFD measurements are likely to be a lumped measurement of SFD in both EW and LW instead of individual values, depending on the exact measurement point locations. Using the Heat Pulse Velocity method, Swanson (1983) found that SFD measurements located close to low conductive boundaries (e.g. LW) can underestimate actual SFD and vice versa for measurement points in LW close to high conductive boundaries (e.g. EW). Circumferential variations in the radial SFD profile were detected in Sample 3 (Fig. 6), but again some of the variations are expected to be due to the measurement point locations in LW. The sequential sensor profile in the northern and southwestern directions did however show differences, confirming the importance of taking multiple circumferential measurements.

4.3. Thermal diffusivity of EW and LW affects SFD estimates

Thermal diffusivity, a critical parameter when determining absolute SFD values by the HRM and HFD methods (Vandegehuchte and Steppe, 2012a), is mainly estimated from the wood moisture content and dry wood density of sapwood. To obtain better estimates in thermal diffusivity of sapwood, the moisture content and wood density should be determined for each sensor location and for both EW and LW. The mean moisture content of 2.49 kg kg$^{-1}$ and wood density of 0.29 kg m$^{-3}$ for EW yielded a lower thermal diffusivity of $1.958 \times 10^{-3}$ W m$^{-1}$ K$^{-1}$, as compared with the mean thermal diffusivity of $2.339 \times 10^{-3}$ W m$^{-1}$ K$^{-1}$ for EW and LW determined from the mean moisture content of 1.38 kg kg$^{-1}$ and wood density of 0.49 kg m$^{-3}$. This can well explain the general underestimation of actual water flux in SC3 which assumed EW and LW were equally water-conductive but thermal diffusivity was that of only EW, despite similar mean absolute errors as compared to SC2 where EW and LW were equally water-conductive and thermal diffusivity was average of EW and LW. The results indicate that not only the hydraulic conductivity but also the thermal diffusivity of both EW and LW needs to be considered when upscaling the whole-tree water use from discrete sap flux density measurements using the HRM and HFD methods. However, extending the moisture content and wood density of EW and LW properties of Sample 4 to all stem samples in the present study may lead to uncertainties for SFD calculations in SC3.
5. Conclusions and recommendations

Conifer species are particular in the way that their hydraulic architecture is made of alternate EW and LW tissues in tree rings, resulting in heterogeneous patterns in hydraulic and heat conductivities, which can affect the point measurements of sap flux density using the HRM and HDF methods. This study has shown that upscaling discrete SFD measurements to whole-tree water use presents several issues in conifers: (i) the actual water flux will be considerably underestimated by considering LW entirely non-conductive. Considering LW with equal hydraulic conductivity as EW will lead to an over- or underestimation of whole-tree water use, but an unbiased estimation in whole-stand transpiration can be achieved by sampling enough trees; (ii) The sap flux is preferentially corrected using radial SFD patterns measured at the same location of the single-point measurement in the same tree, because the radial profile commonly used to upscale discrete SFD measurements in conifers is highly heterogeneous within and among individual trees, which depends to a large extent on the positioning of measurement points in EW or LW areas in the central sapwood and also other factors; (iii) Resolution of the measurements is an issue: a radial SFD profile with 10 mm thermostop coupling was found to be insufficient to confidently capture the radial profile of the studied coniferous species, which can be potentially resolved by ensuring higher-resolution SFD measurements in both EW and LW. Even though the outcome of this study may not be directly transferable to field measurements (i.e., a different force controlling water transport in living trees), it is recommended that similar controlled flow studies are considered prior to commencing field SFD measurements on any tree species. This would not only be of interest to understand the link between the tree hydraulic architecture and the observed sap flow patterns, but also help to improve the accuracy of SFD measurements.

Acknowledgments

The authors would like to thank the laboratory technicians Stewart Matthews and Jason Van der Gevel for their help and advice during the lab experiments. We are also grateful for the assistance given by HQ Plantations when acquiring tree samples and for the feedback from ICT International Ltd. We also acknowledge the constructive comments and suggestions from the associate editor and two anonymous reviewers.

References