ORIGINAL PAPER

Influence of temporospatial variation in sap flux density on estimates of whole-tree water use in *Avicennia marina*

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Abstract

Key message   **Our study shows that sap flow in *Avicennia marina* varies significantly throughout the sapwood and that spatial patterns in sap flux density are dependent on meteorological conditions.**

Abstract   Sap flux density measurements are used worldwide as a relatively inexpensive means to provide estimates of whole-tree and whole-stand water use in forest ecosystems. However, erroneous upscaling from point measurements to the entire sapwood area remains an issue, since sap flow is hardly ever constant throughout the tree. In this study, two widely used sap flow methodologies (the Heat Ratio or HR method and the Heat Field Deformation or HFD method) are used to assess radial and azimuthal variations in sap flux density in three mature trees of the mangrove species *Avicennia marina* in Brisbane, Australia. The genus *Avicennia* is characterised by secondary growth via successive cambia, resulting in an atypical sapwood pattern of xylem patches braided with phloem strings. Water use estimates were calculated in different ways. At first, spatial variation was ignored when upscaling from point measurements. Then, radial and azimuthal variations were incorporated subsequently by measuring at different depths and aspects around the tree. Ignoring azimuthal variation led to over- or underestimations of up to 102 %, while radial variation accounted for discrepancies of up to 25 %. Furthermore, the influence of changing meteorological conditions was assessed, which showed that radial profiles changed in shape during rain events, such that maximum sap flow rates occurred at different depths compared to dry periods. Our study thus indicates that spatial variation in sap flux density is highly unpredictable in *A. marina* due to its hydraulic architecture, and that changing meteorological conditions alter the pattern of this variation. These two factors should be accounted for when assessing whole-tree water use.

Keywords   Temporal variability · Transpiration · Scaling · Sapwood area · Circumferential distribution

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Introduction

Whole-tree and whole-stand water use estimates are of great importance in different aspects of forest science (Wullschleger et al. 1998), which is shown by the fact that they are for instance utilised to resolve water resource management issues (Schiller and Cohen 1995; Dragoni et al. 2005) or to evaluate the role of transpiration in forest hydrology (Barrett et al. 1996; Roberts 2007).

Sap flow measurements are used worldwide to provide these estimates (Steppe et al. 2009, 2010), since they are relatively inexpensive and easy to use, compared to other

approaches such as weighing lysimeters, whole-tree po-
tometers, ventilated chambers or isotope tracers
(Wullschleger et al. 1998). However, most sap flow sensors
provide only one or a few measurement points throughout
the tree, providing information on the sap flux density in
the conducting vessels in the vicinity of the measurement
point (Cohen et al. 2012). Integrating these point mea-
surements over the entire sapwood area may thus result in
over- or underestimations of actual water use when spatial
variations in sap flux density are ignored. As a result, many
have tried to assess radial and/or azimuthal variations in
sap flux density (Hatton et al. 1995; Phillips et al. 1996;
Wullschleger and King 2000; Nadezhdina et al. 2002; Ford
et al. 2004; Fiora and Cescatti 2006; Cohen et al. 2008;
Tsuruta et al. 2010; Shinohara et al. 2013). Most of the
studies on radial variability conclude that sap flux density
reaches a maximum close to the bark and declines towards
the centre of the tree, which makes it a trait that might be
described in many tree species by sampling the radial
profile over a short time period in a limited amount of trees
(Cohen et al. 2012). Azimuthal discrepancies, on the other
hand, are less often accounted for, and the studies that do
incorporate them, frequently find random unsystematic
variation between the different aspects (Lu et al. 2000;
Kume et al. 2012). Others, however, have found a signif-
icant influence of irradiance, leading to lower sap flux
densities at the north side of the tree, since these experi-
ments were conducted on the Northern Hemisphere (Oren
et al. 1999; Shinohara et al. 2013). Structural traits such as
xylem anatomy (Tateishi et al. 2008) or crown architecture
(Lopez-Bernal et al. 2010) have also been shown to have a
crucial impact on azimuthal sap flow patterns which makes
them in most cases much harder to predict than radial
variations (Cohen et al. 2012).

In contrast to most woody plants, including all the
species mentioned in the above studies, that have one
vascular cambium producing xylem to the inner and
phloem to the outer part of the plant stem, the mangrove
genus *Avicennia* has secondary growth via successive
vascular cambia (Zamski 1979; Schmitz et al. 2007). This
reticulate structure of multiple cambia produces a three-
dimensional network of secondary xylem patches braided
with strings of secondary phloem (Robert et al. 2011). This
unusual wood structure is likely to result in even less
predictable and possibly greater spatial variations in sap
flux density. However, since *Avicennia marina* is the most
widespread mangrove species in the world (Spalding et al.
2010), accurate measurements of whole-tree water use are
needed for estimations of water budgets in mangroves.

To our knowledge, only three sap flow experiments have
been conducted in adult *Avicennia* trees so far, one of
which did not account for spatial variations (Becker et al.
1997). Krauss et al. (2007) did evaluate radial patterns in

sap flow for *Avicennia germinans* and noticed sharp
attenuation of sap flux density with radial depth, which
concurs with experiments in species with conventional
wood structure. Muller et al. (2009), however, found that
radial patterns in *A. germinans* were variable, both within
single trees and between different trees, with sap flux
densities sometimes reaching maxima deeper in the stem.
They also observed that the shape of these radial patterns
differed between the wet and dry season of their mea-
surement campaign. However, since sap flux density at
each depth was evaluated with another probe placed at a
different circumferential position, radial discrepancies
could not be distinguished from azimuthal discrepancies.

With the present study we aimed at characterising the
influence of spatial variations in sap flux density, both
azimuthal and radial, on whole-tree water use estimates in
A. marina trees. Furthermore, we wanted to investigate
temporal variation in radial profile due to changes in
meteorological conditions to see if it is possible to
extrapolate spatial variations sampled over a short time
period.

Materials and methods

Site description

The experiment was conducted in a mangrove forest patch
on the bank of the Brisbane River (Brisbane, Queensland,
Australia; 27°30′S–153°01′E). The site has semidiurnal
tides and soil salinity that fluctuates between 5 ppt in the
wet season and 20 ppt in the dry season. *A. marina* (For-
ssk.) Vierh. trees, reaching up to 20 m with an understory
of small *Aegiceras corniculatum* (L.) Blanco shrubs,
dominate the site. Three *Avicennia* trees of different size
were chosen for the experiment, with respective DBHs
(diameter at breast height) of 0.29 (Tree 1), 0.20 (Tree 2)
and 0.10 m (Tree 3). Air temperature, relative humidity of
the air (RH), and rainfall were continuously measured at
the weather station of the St. Lucia campus (University of
Queensland) at a distance of less than 1 km from the study
site. Vapour pressure deficit (VPD) was inferred from air
temperature and RH data and is defined as the difference
between saturation vapour pressure at air temperature and
ambient vapour pressure (Goldstein et al. 1998).

Sapwood depth

To estimate sapwood depth of the studied trees, toluidine
blue dye was injected into the stem base before sunrise (5:00
am) and wood cores were taken from the stem just above the
injection site in the morning (11:00 am). It is then assumed
that the stained part of the wood core represents the living

sapwood, whereas the unstained part represents the heartwood (Mencuccini and Grace 1995). In tree 1, however, significant sap flux densities were recorded with the HFD sensors at depths beyond the sapwood as determined through this methodology. Therefore, sapwood radius was set to 5 mm beyond the deepest measurement point of the HFD sensors. Since no radial profiles were measured for trees 2 and 3 (discussed below), we decided to accept the sapwood depth estimates based on the dye method.

The inaccurate means of determining sapwood area by staining influences the actual water use estimates, but since the focus of this paper is the relative within-tree variation, this does not affect the validity of our observations.

Sap flux density measurements

The trees were equipped with sap flow sensors (ICT International PTY LTD, Armidale, NSW, Australia) of two widely used types: the Heat Ratio Method (HRM) as described by Burgess et al. (2001) and the Heat Field Deformation (HFD) method as described by Nadezhdina et al. (1998, 2012). The HFD sensors provide eight measurement points throughout the tree (ranging from 5 to 75 mm depth with a spacing of 10 mm between them), whereas the HRM sensors only provide two measurement points, at depths of 7.5 and 22.5 mm. Since the bark, which had a thickness ranging between 1 and 1.5 mm for all trees, was not removed, the depths represent the distance from the outside of the tree including the bark. For each type, one sensor was installed at breast height on the north side (N) and one sensor on the south side (S) of tree 1. However, the data from the outer measurement points of the HRM sensors for tree 1 were not included in the results, since they were invalid due to data logger issues. To avoid interference, a horizontal distance of 100 mm was respected between sensors installed at the same side. For trees 2 and 3, HRM sensors were installed, one at each side of the tree (N and S) to account for the azimuthal variation in SFD. Furthermore, since both measurement points were functional, part of the radial pattern could be studied as well.

Sap flux density (SFD) was recorded and stored at a 10-min interval during a 2-month period in 2010: from September 7th to November 9th (DOY 250–313) for tree 1, and from September 16th to October 27th (DOY 259–300) for trees 2 and 3. Sap flow data were analysed with the Sap Flow Tool software package (ICT International PTY LTD, Armidale, NSW, Australia-Phyto-IT, Mariakerke, Belgium).

Spatial variations in sap flux density

To assess possible scaling errors due to spatial variations, we calculated whole-tree water use in different ways: (1) using one measurement point on one side of the tree (tree 1), ignoring both azimuthal and radial variation, or using the mean of the two HRM measurement points on one side of the tree (trees 2 and 3), (2) using the measurements at both sides of the trees, thereby incorporating azimuthal discrepancies, and (3) incorporating the radial profiles obtained with the HFD sensors (only for tree 1), each profile accounting for its half of the tree, hence obtaining the highest spatial resolution and thus the most accurate estimate.

Temporal variations in radial sap flux density profile

Given the higher cost (both financial and power related) of extensive spatial measurements, the influence of short-period sampling of radial profiles on long-term water use estimates was investigated. Therefore, whole-tree water use was calculated based on two subsets of radial profile data. This means that the mean profile measured during a short time period is extrapolated across the whole time span of the experiment, and scaled up with SFDs measured by the HRM sensors. This approximation was then compared to water use based on the actual radial profiles, which are the 10-min profiles measured by the HFD sensors across the whole time span of the experiment, also scaled up with the SFDs from the HRM sensors. To simulate varying sampling periods, we chose two meteorologically different subsets, being a 4-day rainy period (DOY 281–284) and a 4-day dry period (DOY 258–261). We also simulated the worst case scenario sampling periods, by using the radial profiles of the most extreme days of the experiment, being DOY 284 (total rainfall of 44.6 mm and a mean VPD of 0.25 kPa) and DOY 258 (no rainfall and a mean VPD of 2.7 kPa). Weather conditions during the full measurement period are shown in Fig. 1.

Statistical analysis

To analyse differences between sides (N and S), a Wilcoxon signed-rank test was used for every tree, since the Shapiro–Wilk normality test failed ($P < 0.05$), showing that our data were not normally distributed. The same procedure was followed to examine discrepancies between water use estimates with or without incorporating radial profiles. To compare the water use estimates based on the radial profile subsets (rainy and dry period) with the standard estimate based on the actual profiles, a Kruskal–Wallis one-way ANOVA on ranks was executed. The Student–Newman–Keuls method was then used as a multiple comparison procedure to isolate the groups that differed from each other. All these statistical tests were conducted in Sigmaplot 12.0 (Systat Software Inc., Chicago, IL, USA).
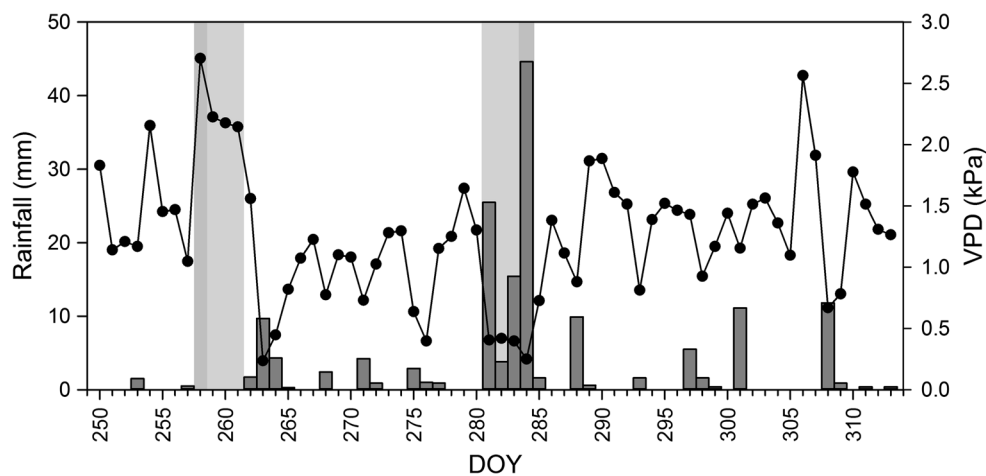
Fig. 1 Meteorological conditions during the measurement period. *Bars* represent daily rainfall whereas *black dots* represent the average daily vapour pressure deficit (VPD). In *grey* are the two chosen periods for the radial profile subsets, the *darker grey* parts represent the most extreme days of the measurement period
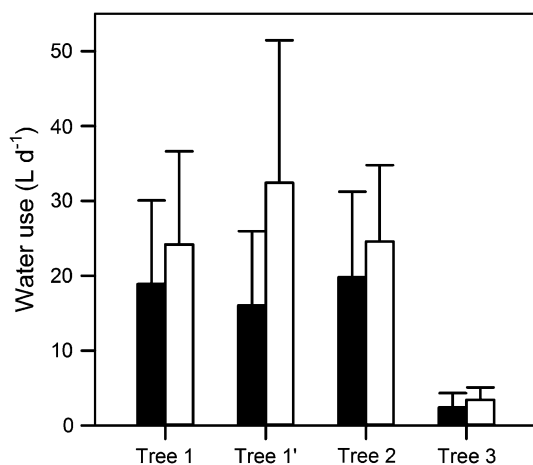
Fig. 2 Comparison of whole-tree water use estimates based on SFD measured at the north side (*black*) and the south side (*white*) in all trees during the measurement period. For tree 1, estimates are provided without (tree 1) and with (tree 1′) incorporation of the radial profiles. For trees 2 and 3 HRM measurements were used. Difference between azimuths was significant for all trees ($P < 0.001$)
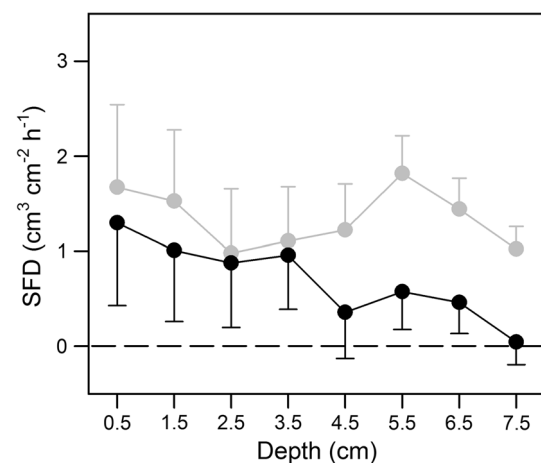
Fig. 3 Mean values ($\pm$SD) of the radial SFD profiles obtained with the two HFD sensors installed in tree 1 during the measurement period (DOY 250–313) for the north side (*black*) and the south side (*grey*). Depth is measured from the outside of the tree (including the bark)

Results

### Spatial variations in sap flux density

For all trees, water use based on measurements on the south side of the tree was significantly higher than that based on the measurements on the north side ($P < 0.001$) with differences ranging from 25 to 102 % (Fig. 2).

Furthermore, measurements with the HFD sensors in tree 1 showed that radial variability in SFD is very high as well, and that it is certainly not constant within the tree. On the north side, a steadily declining pattern was observed, while the south side showed a peak in SFD at a depth of

55 mm in the sapwood (Fig. 3). As a result, there is a significant discrepancy ($P < 0.001$) between water use estimates based on single-point measurements and those incorporating the radial profile, which is also illustrated in Fig. 2. On the north side, the point measurement leads to an overestimation in water use of 17.8 %, since SFD declines towards the centre. In contrast, due to high SFD deeper inside the stem, point measurements underestimate water use by 25.4 % on the south side.

Due to a combination of both radial and azimuthal effects, whole-tree water use estimates for tree 1 ranged from 19 ± 11 L day^{-1} for a single-point sensor to 24 ± 14 L day^{-1} with the highest spatial resolution.

For trees 2 and 3, radial variation was assessed using the two HRM measurement points (Fig. 4). A declining SFD towards the centre of the tree was observed on the south side of both trees, while SFD increased with depth on the north side of the trees.
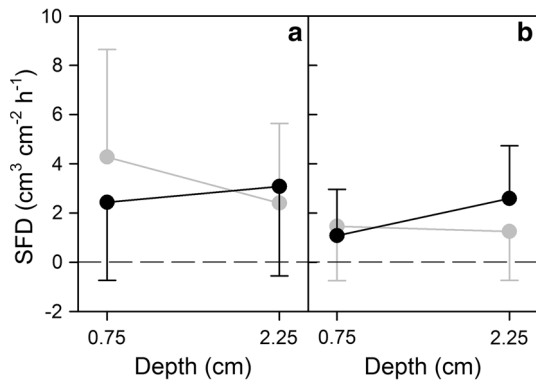

Fig. 4 Mean values (±SD) of the radial SFD profiles obtained with the two HRM sensors installed in **a** tree 2 and **b** tree 3 during the measurement period (DOY 259–300) for the north side (*black*) and the south side (*grey*). Depth is measured from the outside of the tree (including the bark)

Temporal variability in spatial variations

The relative difference in SFD between both azimuths (N and S) remained nearly constant for all trees throughout the whole experiment, and no meteorological dependence was discernible.

On the other hand, radial profiles did change drastically during heavy rain events (Fig. 5). The radial profile did not only shift downwards due to diminished transpiration, but also its shape altered significantly. For example, the absolute maximum in SFD at the south side at a depth of 5.5 cm during dry days (Fig. 5a) becomes a minimum at the time of rainfall (Fig. 5c), and recovers only to a small local maximum in the drier afternoon of this day. On the north side as well, the absolute maximum in SFD in the outer part of the tree (Fig. 5b) disappears during the rain event (Fig. 5d). As a result, water use estimates based on short-term radial profiles measured during rainy periods differed significantly from actual water use estimates, though only on the south side, where it was 12.5 % lower. Narrowing the sample period to one extreme day made this difference even greater, leading to an underestimation of the water use by 50 % on the south side of the tree. On the other hand, water use estimates based on radial profiles

Fig. 5 Diurnal variation of the radial profiles on **a**, **b** a dry day (DOY 258) and **c**, **d** a rainy day (DOY 284) for the south side and the north side of tree 1, respectively
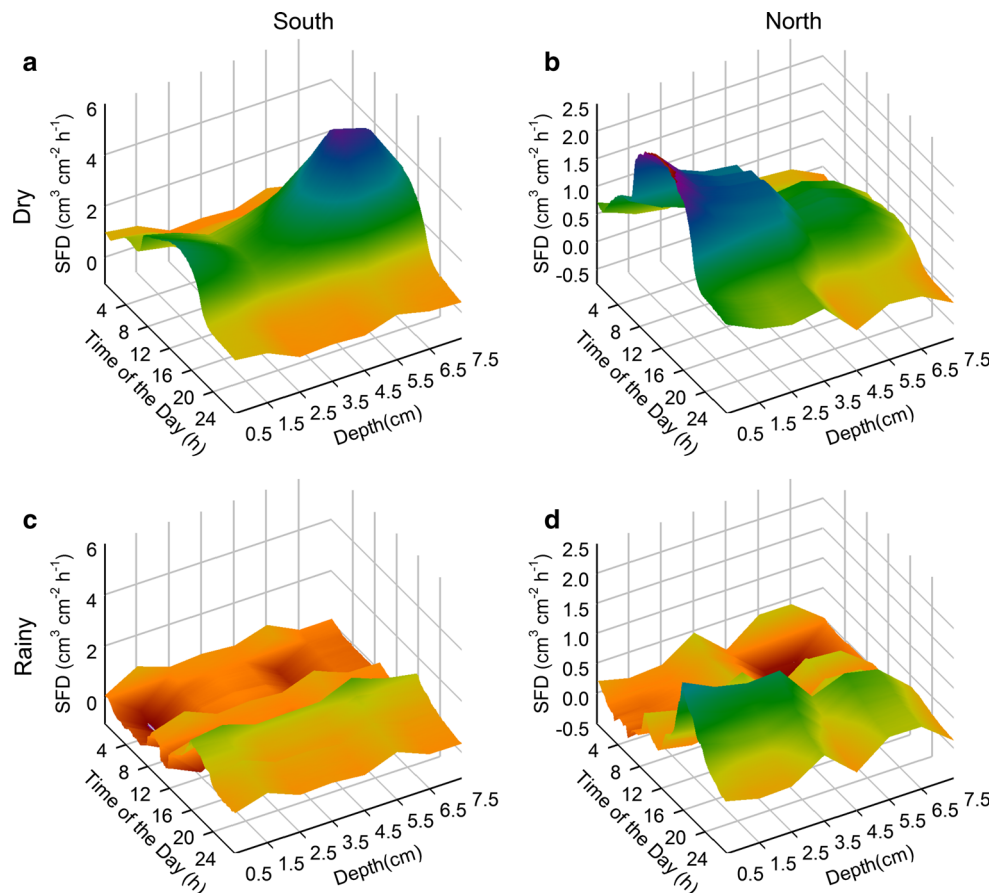
Table 1 Comparison of calculated water use based on meteorologically extreme subsets of the radial profile that have been extrapolated across the whole time span of the experiment, with water use based on the actually measured profiles, for both sides of tree 1

Radial profile	Water use (L day^{-1}) ($\pm$SD)		
	North	South	Total
Dry subset (4 day)	8 ± 5	17 ± 8^a	24 ± 13
Rainy subset (4 day)	8 ± 5	$14 \pm 7^{a,b}$	22 ± 12
Dry day	8 ± 5	17 ± 9^c	25 ± 13^e
Rainy day	7 ± 5	$8 \pm 4^{c,d}$	$15 \pm 9^{e,f}$
Actual	8 ± 5	$16 \pm 10^{b,d}$	24 ± 14^f

For each subset, dry profiles were compared with rainy profiles and both were compared with the actual profiles. No index means no significant difference, whereas values with identical indices differ significantly ($P < 0.05$)

collected in short dry periods differed only slightly (0–6 %) from estimates based on actual profiles. These results are summarised in Table 1.

Besides variability due to rain events, we also observed a diurnal variation in the radial pattern during dry days, especially at the south side (Fig. 5a). SFD is highest at depths of 50, 55 and 60 mm during the day. At night, however, the flow in this part diminishes more drastically than the flow in the outer parts, resulting in a different pattern with a maximum at the outer side of the tree.

Discussion

Spatial variations

It has sometimes been postulated that azimuthal variations can be related to sun exposure, which is consistent with observations that SFD is higher on the south side of the tree (on the Northern Hemisphere) (Oren et al. 1999; Shinohara et al. 2013). Our data also consistently show higher sap flow on the south side for all trees, despite the fact that the experiment was conducted on the Southern Hemisphere and irradiance is, hence, higher on the north side. This indicates that there should be another cause for this discrepancy. One possible explanation is that the river bank was oriented to the south, which might lead to a concentration gradient in soil salinity and, hence, better water availability at the south side, since the river water is less saline than the soil water. Furthermore, due to the fact that the trees close to the river have lower canopies that tend to expand more horizontally towards the open space above the river (instead of growing directly upwards), the examined trees have more room on the south side for canopy development, which was clearly visible for all trees. Lopez-Bernal et al. (2010) indeed showed that crown

architecture plays an important role in the azimuthal distribution in SFD.

Studies looking at radial distribution in sap flow in trees are numerous, as are the types of patterns observed and the possible hypothesised mechanisms to explain them. Cohen et al. (2008) suggested that more embolism and tyloses or smaller vessel diameters in older parts of the sapwood explain the decreasing SFD deeper in the stem. Indeed, this attenuation of sap flow towards the centre has been observed in a large part of the studies on radial variation (Phillips et al. 1996; Wullschleger and King 2000; Delzon et al. 2004; Kubota et al. 2005; Poyatos et al. 2007; Cohen et al. 2008; Kume et al. 2012; Shinohara et al. 2013). A bell-like pattern has often been perceived as well (Lu et al. 2000; Nadezhdina et al. 2002, 2007; Ford et al. 2004; Gebauer et al. 2008; Alvarado-Barrientos et al. 2013), which resembles the steadily declining pattern but with a lower sap flow in the outermost parts of the xylem before a maximum is reached somewhat deeper inside the stem.

The concept of xylem age-related discrepancies is, however, not readily applicable to A. marina, given its unusual wood structure comprising of successive vascular cambia. Due to this exceptional feature, it might be possible that multiple vascular cambia at different depths inside the stem are simultaneously active (Schmitz et al. 2008), making the relationship between depth in the stem and age of the sapwood far from straightforward.

Indeed, although we found a declining pattern at one side of the tree, we found a different pattern at the other side with a distinct maximum at a depth of 55 mm in Tree 1 (Fig. 3). This maximum was especially apparent during dry middays (Fig. 5a), when SFD at depths of 50 and 60 mm was also higher than at the outer measurement points. Although the HRM sensors in trees 2 and 3 only provided two measurement points and thus an incomplete radial pattern, they also confirm that radial patterns are far from constant throughout the tree (Fig. 4). This might be the result of recent cambial activity resulting in highly conducting xylem in the area of high SFD. Since the reticulate network of successive cambia shows a patchy growth, cambial activity can vary between different aspects of the tree which results in optimal growth at distinct moments in time, at different positions around the stem (Schmitz et al. 2008; Robert et al. 2011).

In ordinary trees, which only have one vascular cambium and are thus incapable of this growth mechanism, it has also been shown that radial profiles are influenced by water status in the root system, such that xylem tissue connected to roots with access to readily available water will show higher SFD (Nadezhdina et al. 2007, 2009).

Combining these two hypotheses with our results, one might speculate that the part of the xylem with the highest peak in SFD has a connection to deeper roots with access to

fresh ground water, which will also result in increased cambial activity in this region, allowing for more water transport and growth.

Temporal variability

While it is clear that sap flow is driven by the microclimate, especially the evaporative demand and radiation, only a few studies have investigated the possible influence of the climatic conditions on the shape of the radial SFD profile. All of them concluded that relative contributions at different depths are not constant through varying weather conditions (Nadezhdina et al. 2002; Fiora and Cescatti 2006; Saveyn et al. 2008).

Nonetheless, many studies claim that radial profiles can be sampled over a short time period (Lu et al. 2000; Cohen et al. 2012), and some even suggest taking a one-day profile as a correction for continuous point measurements (Wullschleger and King 2000; Delzon et al. 2004). Our results show that, for *A. marina*, one-day sampling might give a quite accurate estimation, yet caution is needed when choosing the sampling day. Indeed, sampling during heavy rain resulted in a completely different radial profile than sampling during a day with high PAR and VPD (Fig. 5). An absolute decrease is to be expected, since transpiration is diminished during rainy periods. However, in our case the relative differences between the different depths changed as well during rain, resulting in a shift of the location of the highest flow rate. Since our measurement period contained only few days with substantial rainfall, the radial profile obtained during rainy weather resulted in a considerable error. If the experiment had spanned a longer time period (e.g. multiple seasons), the chance of errors occurring due to radial profile sampling would only increase. Hence, we recommend consideration of a longer time period for radial profile sampling, or at least multiple samples throughout different seasons and different weather conditions. When practice (e.g. power supply in remote areas) only allows for short sampling of radial profiles, we would highly recommend sampling during days with weather conditions that are representative of general conditions rather than during extremes.

Conclusions

Our study confirmed that spatial variations in sap flux density should not be ignored when scaling up to whole-tree water use. Furthermore, in contrast to what some studies on other species found, no standard profile can be found in *A. marina*, which is most likely due to its special wood structure. This spatial variation is dependent on meteorological conditions, requiring caution when extrapolating short-term radial profiles over a longer time period. We recommend continuous measurement of multiple radial profiles when circumstances allow it. If not, we suggest sampling multiple profiles around the stem during a period where weather conditions are representative of the overall measurement period to minimise extrapolating errors associated with extreme events. For long-term measurement campaigns, it might be desirable to resample during different seasons.

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