Contribution of sapwood traits to uncertainty in conifer sap flow as estimated with the heat-ratio method

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Abstract

Inferring whole-tree sap flow rates (Q) with thermometric sap flow sensors requires specification of physiological and structural attributes of trees. Using sap temperature measurements to estimate Q with the heat-ratio method (HRM) requires quantification of the water content (m_c), basic density (ρ_b), and depth (R_s) of sapwood. Values of m_c and ρ_b serve to estimate sapwood thermal diffusivity (k), a necessary variable in the calculation of heat-pulse velocity (V_h) that is often set to a nominal value (k_{nom}); m_c and ρ_b are also used to convert V_h to sap velocity (V_s). The sapwood area across which V_s is integrated is often estimated on the basis of R_s . Because m_c and ρ_b are correlated and influence Q through estimation of k and the conversion of V_h to V_s , we sought to quantify the potential error introduced when Q is calculated with k_{nom} rather than with k as estimated from measurements of m_c and ρ_b in five coniferous species. We also examined how variation in m_c , ρ_b , and R_s across sampling scales may contribute to uncertainty in estimated Q . Across the observed range of m_c and ρ_b , the two traits contributed to a net decline in the process of estimating V_s from V_h (with k_{nom}). This suggests that the use of k_{nom} rather than a calculated k may result in overestimation of Q when m_c and ρ_b co-vary as they did in our study. Variability in m_c and ρ_b across sampling scales could induce errors greater than 10% in V_s (and hence Q), while within- and among-tree variability in R_s could impart even greater errors (up to 130%). We propose that this uncertainty be represented in the expression of error in whole-tree sap flow estimates and in statistical analyses involving those estimates.

Keywords: sap flow, heat-ratio method, wood water content, basic density, sapwood area, thermal diffusivity

1. Introduction

Transpiration, the evaporative loss of water from plants through their stomata, is a key component of the terrestrial water balance, influencing streamflow as well as regional convective systems (Ellison et al. 2012). From a plant physiological perspective, transpiration is both a means of avoiding destructive leaf temperatures through evaporative cooling (Schymanski et al. 2013) and a consequence of leaf-to-atmosphere carbon dioxide exchange. Despite its hydrologic and ecological significance, transpiration remains a notoriously challenging process to measure in heterogeneous landscapes. Because transpiration equals liquid-phase flow (i.e., sap flow) when changes in stem water storage are minimal, heat-based sap flow sensors are widely used to estimate sap movement (variously interpreted as sap velocity or sap flux density; Edwards et al. 1997) as a surrogate for transpiration. Sap flow methods differ primarily with regard to the duration of heat emission (i.e., constant or pulse) and the manner of sensing the heat elsewhere in the sap stream (e.g., as time to attain a temperature or as change in temperature at a specified time). In a recent comparison of three sap flow methods, Steppe et al. (2010) documented systematic underestimation of transpiration across methods but observed the least error using a heat-pulse method. Rapid thermal response time (Burgess and Dawson 2008) and detection of reverse flow (Burgess et al. 2001) are further advantages of pulse-based designs.

Applications of sap flow also vary due to the diversity of approaches to inferring tree- or stand-level water flow rates on the basis of point-level observations of heat movement. Transferring observations from the domain of energy to mass of water and from point to tree or stand scales incorporates measurements and assumptions concerning physiological and structural attributes, here termed “auxiliary factors.” While previous studies have related uncertainty in

sapwood area (Hatton et al. 1992), sapwood water content (Vergeynst et al. 2014), and wounding (Moore et al. 2010) to error in sap flow estimates, systematic handling of error remains absent in much of the sap flow literature. The widespread practice of expressing uncertainty in whole-tree sap flow rates as the standard error of the mean (Jung et al. 2011, Ghimire et al. 2014) for the group of interest (e.g., species or age class) omits uncertainty in auxiliary factors and, consequently, may overstate the precision of sap flow estimates. Furthermore, estimating Q involves methodological decisions (e.g., estimation of thermal diffusivity; Vandegehuchte and Steppe 2012) that may mediate the relative importance of error in auxiliary factors. In this study we focus on the widely used heat-ratio method (HRM) design of heat-pulse sensors (Burgess et al. 2001) and examine how methodological decisions and variability in auxiliary factors contribute to uncertainty in tree-level sap flow. First, we provide a brief overview of common practices in using HRM measurements to estimate Q .

1.1. Estimating tree transpiration with the HRM

Heat-ratio method (HRM) sensors track the velocity (V_h) of a heat pulse as a proxy for sap velocity (V_s ; Burgess et al. 2001) and are favored in contexts where physiological or environmental factors result in low or negative V_s (i.e., rootward flow). Specifically, a line heater inserted perpendicularly into the sapwood emits a brief (2.5 s) pulse at each sampling interval (e.g., half-hourly), resulting in a temperature rise recorded by thermocouples positioned up- and downstream of the heater. V_h (cm h^{-1}) is then calculated as

$$V_h = (k/x) \ln(v_d/v_u) 3600 \text{ s h}^{-1}, \quad (\text{Eqn. 1})$$

where x is heater-to-thermocouple spacing in the axial direction (cm), k is sapwood thermal diffusivity ($\text{cm}^2 \text{ s}^{-1}$), and v_u and v_d are the respective up- and downstream temperature rises ($^{\circ}\text{C}$)

at a specified time after the pulse (60-100 s) . Following Burgess et al. (2001), researchers typically set k to a nominal value of $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ (hereafter k_{nom}), which is intermediate between thermal diffusivities of water ($1.4 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$) and of dry wood ($4.0 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$), as originally noted by Marshall (1958). Burgess et al. (2001) also outline a procedure for calculating a theoretical k (k_{Burg}):

$$k_{Burg} = 10^5 K_{gw} / (\rho_{gw} c_{gw}), \quad (\text{Eqn. 2})$$

where K_{gw} is thermal conductivity ($\text{J m}^{-1} \text{ s}^{-1} \text{ }^\circ\text{C}^{-1}$), ρ_{gw} is density (kg m^{-3}), and c_{gw} is specific heat capacity ($\text{J kg}^{-1} \text{ }^\circ\text{C}^{-1}$) of green wood (i.e., living sapwood). K_{gw} and c_{gw} are estimated as linear mixtures of the properties of water and dry wood (Burgess et al. 2001, Vandegehuchte and Steppe 2012) on the basis of sapwood water content, m_c (kg kg^{-1}), and basic density, ρ_b (kg m^{-3}). Sapwood water content, m_c , is defined as $(w_f - w_d) / w_d$, where w_f and w_d are the fresh and oven-dry weight (kg) of a sapwood sample, and ρ_b is the ratio of w_d to sample volume, vol (m^3).

In common practice, V_h is calculated immediately after measurement of v_u and v_d using k_{nom} , which may later be replaced with k_{Burg} or k as estimated using the method of Vandegehuchte and Steppe (2012; k_{Vand}). The latter method accounts for the difference in thermal conductivity of free water compared to water bound to the wood matrix. As V_h is directly proportional to k (Eqn. 1), differences between k_{Burg} (or k_{Vand}) and k_{nom} induce the same magnitude of error in V_h .

Because V_h represents both convection (i.e., sap movement) and conduction of heat through the wood matrix (Marshall 1958), analyses rarely involve V_h itself, but rather V_s (cm h^{-1}), which is given as:

$$V_s = V_h \rho_b (c_w + m_c c_s) / \rho_s c_s, \quad (\text{Eqn. 3})$$

where c_s and c_w refer to the specific heat capacities of sap and wood, respectively, and ρ_s is the density of sap; c_s , c_w , and ρ_s are treated as constants (Burgess et al. 2001). Hence, m_c and ρ_b influence HRM transpiration estimates first through the calculation of k_{Burg} or k_{Vand} (Eqn. 2) and subsequently through the conversion of V_h to V_s (Eqn. 3). Therefore, the sensitivity of V_s to error in m_c and ρ_b depends on the net behavior of these variables in both steps (Fig. 1).

Whole-tree sap flow, Q (volume of water per tree per unit time), is obtained by integrating V_s radially and circumferentially across the cross-sectional sapwood area, A_s . To estimate water fluxes beyond the tree level, Q can be normalized by A_s , yielding sap flux density, J ($\text{cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$). In turn, J is multiplied by stand sapwood area to estimate stand-level water flow. At the tree or stand level, A_s may be predicted as an empirical function of diameter at breast height, DBH (cm), or calculated using DBH and sapwood depth, R_s (cm), assuming a circular or elliptical trunk cross-section. Upon removal or replacement of sensors, probe misalignment and the size of wound tissue in sapwood adjacent to probes can be measured in order to correct the systematic errors discussed in Burgess et al. (2001).

1.2. Study objectives

Sap flow studies and recent research on woody plant functional traits (e.g., Chave et al. 2009) have revealed considerable variability in each of the auxiliary factors (“Inputs” in Fig. 1). Yet because sensor design and datalogger limitations result in sampling tradeoffs, consideration of variability in all the aforementioned factors is rare in practice. For instance, among-tree replication is often prioritized over within-tree replication (e.g., Hu et al. 2010, Dalsgaard et al. 2011, Angstmann et al. 2012), as supported by Ford et al. (2007). Furthermore, auxiliary factors are often estimated using sapwood samples obtained from trees co-occurring with HRM-

instrumented trees to avoid tissue damage and additional measurement error (Jung et al. 2011, Gebauer et al. 2008). In studies with the objective of estimating total volume of water transpired at the stand or catchment scale (e.g., Delzon and Loustau 2005, Zeppel et al. 2008), uncertainty in tree-level transpiration may result in large errors at the scale of interest. Using a typical HRM sensor design and a sampling scheme developed to address watershed-scale objectives, we sought to quantify the uncertainty in Q due to variability in sapwood properties, including R_s , while also focusing on m_c and ρ_b in light of the widespread use of k_{nom} rather than k_{Burg} or k_{Vand} . We address three specific objectives through empirical and theoretical means:

- 1) Determine how simultaneous variation in m_c and ρ_b contributes to error in V_s
- 2) Quantify the uncertainty in sap flow incurred through the measurement of m_c , ρ_b , and R_s , across spatial scales, from within individual trees to across sites
- 3) Assess how uncertainty in tree-level Q affects inferences across sites and species

Taken together, these objectives represent an initial effort to prioritize sampling of sapwood properties to reduce errors in sap flow-based estimates of transpiration.

2. Materials and methods

2.1. Study site

We conducted our study at Lubrecht Experimental Forest (LEF; 47° N, 113° W), a University of Montana research station located 54 km northeast of Missoula, Montana. Data collection at LEF centered on four long-term monitoring sites we established in summer 2013 in the 18-km² watershed of the North Fork of Elk Creek. At low (1400 m) and high (1800 m) elevations, we selected one north-facing and one south-facing convergent hillslope for our study; this resulted in

a total of four hillslopes across the watershed. All four hillslopes featured an assemblage of conifers dominated or co-dominated by Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Co-occurring species included ponderosa pine (*Pinus ponderosa*) and western larch (*Larix occidentalis*) at lower elevation, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) at higher elevation. As a result of extensive timber harvest prior to the 1940s, the stands at all sites were relatively uniform in age (approximately 70-80 years old). To more thoroughly characterize uncertainty in sap flow estimates due to the variability of scale factors within trees, stands, and sites (Objective 2), we also measured m_c , ρ_b , and R_s in Douglas-fir in two additional 1800-m sites near Bozeman, Montana (henceforth BZN), 225 km southwest of LEF. At BZN, we selected one north- and one south-facing site, both of which were dominated by second-growth Douglas-fir of similar DBH (30-40 cm) and stature (15-20 m) as Douglas-fir growing at the LEF sites. LEF and BZN sites were each subdivided into two 20 m-diameter plots. Due to systematic differences in how plots were established at LEF versus BZN (i.e., one plot in the convergent hollow and one on adjacent the slope of each LEF site and all plots on consistently gentle slopes at BZN), this study focuses more on variation across sites and species than between plots.

2.2. Field measurements

2.2.1. Sap flow. We estimated V_h using HRM sensors (Burgess et al. 2001) that we constructed according to Hu et al. (2010). In this implementation of the HRM, a 3.7-cm nichrome line heater (18-20 Ω) was inserted perpendicularly into the sapwood at a height of 1.3 m. Thermocouple probes positioned 0.6 cm up- and downstream of the heater provided temperature measurements at depths of 2 cm and 3.7 cm into the sapwood. For each sapwood depth, V_h was calculated as a

function of v_d and v_u (*sensu* Eqn. 1) at 60 s after a 2.5-s heat pulse, with $k = k_{nom}$ ($2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$) and $x = 0.6 \text{ cm}$. We logged the V_h data using CR1000 dataloggers (Campbell Scientific Inc., Logan, UT), equipped with an AM4/16 multiplexer (Campbell Scientific).

In each of the four LEF hillslope sites, we installed HRM sensors in four dominant individuals of Douglas-fir and four of either ponderosa pine, subalpine fir, Engelmann spruce, or western larch, pairing Douglas-fir with a different species at each site (i.e., $n=16$ for Douglas-fir and $n=4$ for all others). Each tree received one probe set on the east side of the trunk and one on the west. We selected trees to prioritize crown symmetry and site-level representativeness of DBH. The following analyses were conducted on a V_h dataset from May and August 2014.

Error in the position of the thermocouples in an HRM probe set can introduce major bias in calculated V_h (Burgess et al. 2001). Researchers often address this type of error by measuring probe misalignment in situ or by applying an offset to each V_h time series. We accounted for misalignment by assuming zero flow during the night (0:00 to 5:00 h) and during conditions of low vapor pressure deficit (VPD). We tested how varying the VPD threshold would affect the determination of the zero-flow offset by defining different maximum VPD values from 0 to 1 kPa, resampling the V_h measurements from these subset periods to obtain equal numbers of observations, and then averaging the resampled measurements to generate the offsets. Among the thermocouple pairs for which the VPD threshold significantly affected the resulting offsets (i.e., non-zero slope of offset values against threshold values), the mean change in the offset was only 0.06 cm h^{-1} per 0.1 kPa change in the threshold. We therefore averaged the offsets for each thermocouple pair and then subtracted them from the corresponding time course of V_h .

Because tissue wounding at the installation site reduces flow in the xylem surrounding the probe set, recorded V_h is typically adjusted through second- or third-degree polynomial

equations, yielding corrected heat-pulse velocity V_c (cm h^{-1}). Wound size, measured after probe removal, is incorporated into the polynomial correction through the choice of coefficients (Swanson 1983, Burgess et al. 2001). While past studies have applied a minimum wound correction when wound size data were unavailable (e.g., Ambrose et al. 2010), the magnitude of wound size can impart greater than two-fold differences in V_c at moderate values of V_h (20-30 cm h^{-1}) due to the nonlinearity of the correction equations. Because we did not have wound measurements for the study period and consequently estimated flow rates from uncorrected V_h , we note that the rates reported here should be interpreted as relative rather than absolute values.

To express sap flow volumetrically, we divided the measured domain into two concentric rings, such that the thermocouple positions defined the midpoints of the rings, and then multiplied V_s at each thermocouple position by the area of its corresponding sapwood ring (Hu et al. 2010). In light of within-tree variability in R_s and bark depth and our use of fixed-length probes (3.7 cm), the thermocouples represented varying radial fractions of sapwood; again, we note that our estimates of Q are approximate. In cases where probes recorded apparent flow deeper than R_s , we redefined the positions of the outer and inner thermocouples as 50 and 90% of R_s . Conversely, when R_s exceeded the length of the probe, we extrapolated V_s in the remaining sapwood by assuming a linear decline from the inner thermocouple position (3.7 cm) to the sapwood-heartwood interface, such that V_s in the heartwood was assumed to be zero. In estimating Q , we set V_s equal to recorded V_h (i.e., calculated with k_{nom}) so that sapwood-related errors may be expressed volumetrically by multiplying Q by the relative error terms described below.

2.2.2. Auxiliary factors. Of the measurements required to estimate Q from observations of v_d/v_u (Fig.1), we focused on m_c and ρ_b in order to characterize the sensitivity of V_s (and hence Q) to

uncertainty in these variables (Objective 1) and also to address how cross-scale variability in m_c and ρ_b as well as R_s contributes to uncertainty in Q (Objective 2). To estimate m_c and ρ_b from w_f , w_d , and vol , we used a 5.15 mm-diameter increment borer (Haglöf Sweden AB) to collect xylem samples at breast height from trees co-occurring with sap flow trees at LEF in May and August 2014 ($n=20$, $n=48$, respectively; see Table 1 for n by species) and from Douglas-fir individuals in the BZN sites in October and November 2014 ($n=16$). At LEF, we took one core per tree and separated the core into two samples representing xylem over radial depths of 0-2 and 2-4 cm. In individuals with R_s less than 2 cm (e.g., western larch, subalpine fir, and sometimes Douglas-fir), the 0-2 cm sample reflected a weighted average of sapwood and heartwood, and the 2-4 cm was purely heartwood. We did not isolate sapwood when R_s was less than 2 cm because v_d/v_u readings in the measured domain (2-3.7 cm) are likely influenced by the properties of heartwood in such cases. To standardize the comparisons in this study, we limited our analyses to the 0-2 cm fraction of sapwood. In each of the four BZN stands, we cored each of four Douglas-fir trees from the four cardinal directions and collected the fraction of each core representing radial depths 0-2 cm. We used digital calipers (resolution +/- 0.03 mm) to measure core length and diameter at two positions immediately after sampling to calculate vol and control for potential effects of wood expansion and contraction on ρ_b . Core samples were subsequently placed in glass vials, capped and sealed with Parafilm M® to prevent evaporation. Vials were weighed with samples, dried at 70° C for 48 h, and reweighed with and without samples to determine w_f and w_d . We used w_f , w_d , and vol to calculate m_c and ρ_b for use in the analyses.

We measured R_s and bark thickness (*bark*, cm) on the east and west sides of all sap flow trees ($n=32$) and co-occurring trees ($n=48$) at LEF using the increment borer and calipers. In general, it was possible to distinguish the sapwood-heartwood interface by noting the depth at

which wood opacity increased, though the interface was more diffuse in Engelmann spruce and ponderosa pine than in the other species. R_s and $bark$ were also measured in the four cardinal directions in the BZN trees ($n=16$). Assuming a circular stem, A_s was calculated as:

$$A_s = \pi(\text{DBH}/2 - bark)^2 - \pi(\text{DBH}/2 - bark - R_s)^2 \quad (\text{Eqn. 4}).$$

2.3. Analyses

2.3.1. Objective 1. To quantify the effects of m_c and ρ_b on the estimation of V_s , we defined three coefficients: k_{Burg}/k_{nom} , k_{Vand}/k_{nom} , and V_s/V_h . The first two coefficients express theoretical thermal diffusivity as a proportion of the nominal value, while the third term is the ratio of sap velocity to heat-pulse velocity. In converting recorded V_h (with k_{nom}) to V_s , the net proportional effect, N , of m_c and ρ_b , may thus be defined as the product of the thermal diffusivity coefficient (k_{Burg}/k_{nom} or k_{Vand}/k_{nom}) and the sap velocity coefficient (V_s/V_h). N is expressed calculated V_s as a proportion of V_h as recorded in the field; for example, when N is 0.5, estimated V_s will be half the value of recorded V_h , while N of 1 indicates that V_h and V_s are equal (i.e., the case that we assumed above in estimating a reference Q).

For combinations of m_c and ρ_b yielding estimates of k_{Burg} (or k_{Vand}) close to k_{nom} , k_{Burg}/k_{nom} (or k_{Vand}/k_{nom}) approaches 1, and recorded V_h may be used to estimate V_s without modification. Marshall (1958) notes that V_h should be less than V_s since V_h includes heat transfer through both sap and the wood matrix while V_s is only a measure of convection through sap; hence, we may expect $V_s/V_h > 1$. To determine how the thermal diffusivity coefficients vary through m_c - ρ_b trait space, we calculated the sapwood water contents (m_c) that would yield a particular coefficient value across range of sapwood density (ρ_b) values. This was accomplished by using the uniroot function in R version 3.2.0 (R Core Team 2015) to solve Eqn. 2 and the

thermal conductivity (K_{gw}) calculations included in Burgess et al. (2001) and Vandegehuchte and Steppe (2012) for m_c given k_{Burg} (or k_{Vand}) and ρ_b . Similarly, we rearranged Eqn. 3 to solve for m_c and then calculated the value of m_c that would yield a particular ratio of V_s to V_h across the range of ρ_b . Repeating this for multiple values of V_s/V_h allowed us to generate isolines of the three coefficients, onto which we overlaid the sapwood core data to explore how m_c changes with respect to ρ_b and, simultaneously, the effects of this bivariate distribution on the estimation of the coefficients.

To further quantify the net effect of m_c and ρ_b on V_s , considering methodological uncertainty (choice of k estimation method) as well as random variability in m_c and ρ_b , we conducted a simulation constrained by the field measurements from LEF. In R, we simulated 10,000 sets of m_c , ρ_b , and V_h (as calculated with k_{nom}) for each of the five species. Each variable set was generated by first sampling a value of ρ_b from a uniform distribution defined by the range of ρ_b values observed in the sapwood cores for each species (Table 1). To incorporate the correlation between m_c and ρ_b into the simulation, we modeled m_c using the ρ_b value as a predictor in a species-specific simple linear regression (Table 1). An error term was then sampled from a normal distribution with a mean of zero and a standard deviation estimated from the residuals of the m_c - ρ_b regression (Table 1); this error term was added to the modeled m_c value to account for variability about the linear relationship between the two variables.

Each variable set also included a value of V_h sampled as follows. After subtracting an offset from each time series of V_h to account for misalignment, we aggregated the readings for each tree on each day by averaging the half-hourly readings of V_h between 9:00 and 18:00 h, resulting in species-specific sets of daytime V_h values buffered against outlying observations. As with the sapwood core samples, we restricted this data reduction step to the time series from the

outer thermocouple pair (2 cm radial depth) in order to maintain consistency in cross-species comparisons., A value of V_h was sampled from the set of daytime mean V_h values corresponding to each species for each iteration of the simulation.

Finally, we used the simulated variable sets to calculate k_{Burg}/k_{nom} , k_{Vand}/k_{nom} , and V_s/V_h . We determined the net effect of m_c and ρ_b using the two methods of calculating thermal diffusivity (N_{Burg} and N_{Vand}), which we then multiplied by the simulated V_h to obtain $V_{s_{Burg}}$ and $V_{s_{Vand}}$. The relative error incurred through the use of k_{nom} rather than k_{Burg} (or k_{Vand}) was calculated as the difference between k_{nom} and k_{Burg} (or k_{Vand}) divided by k_{Burg} (or k_{Vand}). Hence, a positive relative error indicates overestimation.

2.3.2. Objective 2. Our second objective was to quantify how variability in m_c , ρ_b , and R_s across spatial scales imparts uncertainty to estimates of Q . We developed a hierarchical resampling scheme in order to estimate the error that may be incurred in Q when sapwood traits (i.e., m_c , ρ_b , and R_s) are measured at locations other than the point of sap flow probe installation, such as at another point in the same trunk, in a co-occurring tree, in a neighboring stand, or at a different site. We employed the nested dataset of Douglas-fir sapwood traits measured at the BZN sites (4 cores per 4 trees per 2 stands per 2 sites) for the analysis of m_c and ρ_b and within-tree variation in R_s and used all the measurements of R_s in Douglas-fir at BZN and LEF sites to estimate errors associated with use of a regression to predict A_s based on DBH.

For each sapwood core sample from BZN, we estimated the net scaling effect of m_c and ρ_b for both methods of estimating k (N_{Burg} and N_{Vand}). Then, designating the estimated N_{Burg} (or N_{Vand}) as the true value for each sample, we quantified what the relative error would be if we were to use a value from a different sample as a surrogate for the true value. By drawing the surrogate samples from multiple scales (within the same tree, within the same plot,

within the same site, and from a different site) and then averaging the absolute value of the errors within each of those scales, we obtained estimates of how this core-for-core substitution could affect uncertainty in converting V_h to V_s .

In a similar manner, we assumed that “true” A_s for each tree was the average of A_s calculated using R_s and bark depth measured on each of four cores (Eqn. 4) and then quantified the relative error in A_s if we had used only one, two, or three cores for the calculation. To quantify within-species relative error with the dataset of Douglas-fir A_s at both BZN and LEF, we omitted one tree at a time, fit a simple linear regression to predict A_s as a function of DBH, and then divided the difference between regression-predicted A_s and R_s -calculated A_s by the calculated A_s value.

2.3.3. Objective 3. We developed a resampling-based analysis to explore how uncertainty in the estimation of tree-level Q can affect inferences on intra- and interspecific variation in water use. In this procedure, we iteratively converted representative diurnal time series of V_h to whole-tree Q and then applied Tukey’s HSD test to estimate differences in Q across sites (in Douglas-fir) and between co-occurring species (i.e., Douglas-fir and the paired species at each site). First, for each tree, we selected days with complete sets of V_h (i.e., 48 half-hourly measurements at outer and inner sapwood depths for at least one probe set) from 14 rain-free days in August. To represent uncertainty in Q due to circumferential variation in V_h , we separately prepared time series for the east and west side of each tree and, when both sides were available, for the mean of the two sides. We then calculated the average half-hourly V_h for each tree at each measurement interval, resulting in 1-3 diurnal time series for each tree. Finally, we used each time series to estimate the daily sum of Q ($\text{L tree}^{-1} \text{ day}^{-1}$) with a conventional approach (using k_{nom} , species-mean m_c and ρ_b , and the species-specific regression of R_s on DBH) and with an approach

accounting for uncertainty in auxiliary factors (using k_{Burg} or k_{Vand} , m_c and ρ_b resampled as in Section. 2.3.1, and a species-specific regression of R_s on DBH plus resampled residuals *sensu* Magnussen and Burgess 1997). By repeatedly resampling auxiliary factors (100 times per half-hourly V_h time series) and then estimating Q , we obtained multiple distributions of daily Q for each tree that collectively represent the random error and methodological uncertainty in auxiliary factors. To determine how the spread of the resultant tree-level distributions of Q may affect statistical inferences at broader scales, we conducted Tukey's Honestly Significant Difference (HSD) test to estimate differences in Q between co-occurring species and in Douglas-fir across sites, drawing one sample per distribution and performing the test 100 times.

3. Results

3.1. Field measurements

The five coniferous species exhibited wide ranges of V_h , m_c , and ρ_b (Table 1, Fig. 2). Maximum daytime-averaged V_h ranged from 6.3 cm h⁻¹ in subalpine fir to 41.3 cm h⁻¹ in western larch. Negative daytime-averaged V_h values (Table 1) were observed in all five species during rain events in August. Estimated whole-tree water use, Q , ranged from an average of 1.9 L tree⁻¹ day⁻¹ (SE: 0.9) in subalpine fir to 40.7 L tree⁻¹ day⁻¹ (SE: 8) in Douglas-fir.

A high degree of intraspecific variability was detected in m_c (e.g., three-fold variation in Engelmann spruce), while ρ_b varied by a factor of about 1.5 within each species. Variability in m_c appeared to be linked to sample-to-sample differences in ρ_b within each species, with the exception of subalpine fir (adjusted $R^2 = 0.06$ from the regression of m_c against ρ_b ; Table 1). The slope of the m_c - ρ_b relationship did not appear to differ among species (p -value = 0.5).

After m_c and ρ_b , the third auxiliary factor of primary interest was sapwood depth, R_s . Measurements of R_s revealed a positive relationship with DBH across species (Fig. 3A). Though the slope of the R_s -DBH relationship did not differ significantly across species (p -value = 0.5), ponderosa pine and Engelmann spruce were distinguished from the other three species in the rate with which A_s (as calculated with R_s) increased with DBH (p -value < 0.0001, Fig. 3B).

3.2. Analyses

3.2.1. Objective 1.

Because the coefficients k_{Burg}/k_{nom} , k_{Vand}/k_{nom} , and V_s/V_h are each determined numerically on the basis of m_c and ρ_b , the isoline plots (Fig. 2) and simulation results (Fig. 4) indicate how various combinations of m_c and ρ_b would affect the procedure of converting recorded V_h to V_s . Due to the correlation of m_c and ρ_b in the sapwood core samples, the coefficient values did not vary substantially within each species (Fig. 2). In other words, the potential effect of m_c or ρ_b on the scaling procedure was partially offset by variability in the other variable, such that variability in the scaling coefficients was restricted across the observed range of m_c and ρ_b . Across the five species, k_{Burg}/k_{nom} reached a minimum of 0.48 and a maximum of 0.70 (mean=0.55, SE=0.01), while k_{Vand}/k_{nom} ranged from 0.73 to 0.97 (mean=0.82, SE=0.01) and V_s/V_h ranged from 0.60 to 1.27 (mean=0.96, SE=0.02).

The variability incorporated into the simulated sets of m_c , ρ_b , and V_h permitted exploration of trait space beyond the region directly observed in our study. Consequently, our results indicate the conditions under which the outcomes of the V_s estimation procedure follow theoretical expectations (i.e., when calculated k approaches k_{nom} and when $V_s > V_h$; Marshall 1958). The scaling coefficients k_{Burg}/k_{nom} and k_{Vand}/k_{nom} were greater than 1 for only

<0.001% and 0.01% of variable sets, respectively. These sets featured much lower m_c (mean = 0.72 kg kg⁻¹, SE = 0.01) than observed in the core samples (mean = 1.85 kg kg⁻¹, SE = 0.05). The decline in calculated k with increasing m_c (Fig. 4A) resulted in a species-specific relationship between m_c and relative error in V_s (Fig. 4B), with greater sensitivity and possible error when k was calculated according to Burgess et al. (2001).

The distribution of V_s/V_h in m_c - ρ_b space was similar to that of the thermal diffusivity coefficients: a simultaneous decrease in ρ_b and increase in m_c could result in no change in V_s/V_h (Fig. 2C). However, because V_s/V_h increases with ρ_b and m_c in Eqn. 3, V_s/V_h varies inversely with the thermal diffusivity coefficients (Fig. 4C). Analysis of the net effect of the two scaling coefficients, N , indicated an overall positive effect of m_c in scaling from V_h to V_s (i.e., V_s approaches V_h with increasing m_c ; Fig. 4D) despite the negative influence of m_c on k_{Burg}/k_{nom} and k_{Vand}/k_{nom} . Using both methods of estimating k , the process of estimating V_s resulted in an overall decline from simulated V_h (with k_{nom}) and a reduction in intraspecific variability of velocities (Fig. 5). In other words, incorporating the variability in ρ_b and m_c into the calculation process has a homogenizing effect on the distribution of velocities within each species.

3.2.2. Objective 2. In light of the effects of ρ_b and m_c on sap flow estimation, we sought to quantify the possible errors associated with the common practice of measuring these traits and R_s at sampling scales other than in the exact position of the sap flow probe with which Q will be estimated. To address this objective, we analyzed the nested dataset of Douglas-fir traits. Due to core-to-core differences in the net effect of ρ_b and m_c , N (i.e., where each core falls in relation to the isolines in Fig. 2), the use of one core as a proxy for ρ_b and m_c at another position in the same tree could impart relative errors of up to 0.137 when using k_{Vand} and 0.089 when using k_{Burg}

(Fig. 6). As we shifted the scale from which the surrogate core was taken (i.e., from the same tree, from other trees within the same plot, from another plot within the same site, or from a different site), the maximum error remained relatively consistent, but the minimum error increased. At the broadest scale within our analysis, the use of ρ_b and m_c measurements obtained at one site as surrogates for the same variables in a tree at a different site resulted in an average relative error of 0.115 when using k_{Vand} and 0.078 when using k_{Burg} .

Though we were not able to obtain absolute measurements of cross-sectional A_s for the study trees, our dataset permitted us to assess how the number of R_s measurements would affect the range of possible A_s estimates for a particular tree (Fig. 7A) and what errors may result from the use of a regression to predict A_s based on DBH (Fig. 7B). When only a single core was used to estimate A_s , the error relative to the four-core mean A_s ranged from 0.05 to 0.42. The range of error in A_s declined as the number of cores increased, but errors of up to 0.15 were possible even when three cores were used. The species-specific regression of A_s on DBH yielded even larger errors, with a maximum relative error of 1.3 and a mean of 0.31 (SE=0.03).

3.2.3. Objective 3. Iteratively incorporating uncertainty into the estimation of Q yielded a wide range of possible distributions for Q for each tree (Fig. 8). As a result, a range of statistical inferences may be drawn. Surprisingly, differences in Q between co-occurring species were more frequently detected with Tukey's HSD test when Q for each tree was represented by a resampling-based distribution rather than by a single point estimate. When comparisons were conducted on point estimates of Q (calculated with k_{nom} , species-mean values of ρ_b and m_c , and an errorless species-specific regression of R_s on DBH), only one significant difference was detected. Douglas-fir was estimated to use 54 L more water per tree per day than subalpine fir (p -value=0.03; 95% confidence interval: 7-100 L tree⁻¹ day⁻¹) when Q was estimated from east-side

probe sets. In contrast, 8 comparisons were significant (i.e., p -value < 0.05) when the test was applied to samples drawn from the distribution of Q for each tree: Douglas-fir was found to differ from Engelmann spruce and western larch, as well as subalpine fir. However, the former two species were found to significantly differ from Douglas-fir in fewer than 40% of cases. No significant differences in Q were detected in Douglas-fir growing across sites using either method of analysis.

4. Discussion

Sap flow sensors are widely used in hydrological and ecological studies to estimate whole-tree sap flow, Q , on the basis of the movement of heat through the sap stream. Statistical inferences on tree water use are made after the proxy measurement (e.g., temperature rise in the sap stream, in the case of the heat-ratio method) is converted to V_s and Q , which involves numerous avenues for the introduction and propagation of error. Variability in the physiological and structural data required for estimating Q and their relative effects on uncertainty in the final estimate have been addressed in previous sap flow studies (e.g., Hatton et al. 1992, Bleby et al. 2004, Ford et al. 2007, Muñoz-Vilers et al. 2012, Alvarado-Barrientos et al. 2013, Gotsch et al. 2014). However, published sap flow error analyses have generally followed a one-at-a-time approach, assessing each source of error individually and hence ignoring interactive and compounding effects. In light of the rarity of explicit treatment of error in typical sap flow applications and in consideration of the established sensitivity of sap flow methods to variability in wood water content, m_c (López-Bernal et al. 2014, Swanson 1983), we developed an approach to characterize the uncertainty in sap velocity, V_s (and hence Q), attributable to m_c and wood density, ρ_b , while also acknowledging species-specific relationships between the two-variables.

We also pursued the complementary objectives of quantifying how variability in m_c , ρ_b , and sapwood depth, R_s , across sampling scales may contribute error to estimates of Q and of determining how uncertainty in these auxiliary factors may affect statistical analysis of species- and site-level differences. Our findings can help prioritize efforts to sample auxiliary factors and improve confidence in estimates of Q and related analyses.

4.1. The use of a nominal value for thermal diffusivity overestimates heat-pulse velocity and whole-tree water use.

Sap flow measurements depend on the thermal properties of sapwood (K_{gw} , ρ_{gw} , and c_{gw}), which are sensitive to variation in m_c and ρ_b (Swanson 1983). Recent studies (e.g., Vergeynst et al. 2014, López-Bernal et al. 2014, Vandegehuchte and Steppe 2012) have stressed the importance of accurately quantifying m_c in order to reduce errors in sap flow estimates. However, m_c and ρ_b do not vary in isolation (Fig. 2), and these variables affect estimation of sap flow calculations not only through the estimation of thermal diffusivity (k) but also in the conversion of heat-pulse velocity (V_h) to V_s . Furthermore, the relative importance of the two variables to the scaling process may depend on methodological decisions, namely the selection of a value for k (use of a nominal value or calculation following the methods of Burgess et al. 2001 or Vandegehuchte and Steppe 2012). We found that V_s ranged from 0.31 to 1.2 times V_h as calculated with k_{nom} (Fig. 4D) when we evaluated the sensitivity of sap flow calculations to simultaneous variation in m_c and ρ_b . This proportion (N) represents the effect of substituting calculated k (k_{Burg} or k_{Vand}) for k_{nom} and distinguishing sap movement from conduction through the wood matrix (Eqn. 3).

Although Burgess et al. (2001) presented a method for estimating k based on m_c and ρ_b , the use of k_{nom} remains widespread in practice (e.g., Alvarado-Barrientos et al. 2013, Hu et al.

2010). This value ($2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$) first appeared in the work of Marshall (1958). Burgess et al. (2001) reported obtaining values similar to k_{nom} through the calculation of k for *Banksia prionotes* (an angiosperm) and by solving Eqn. 1 for k with independent measurements of V_h , implying that the use of k_{nom} would not impart major errors to transpiration estimates. Our simulation indicated that calculated k approached k_{nom} only at low m_c , with greater discrepancy between k_{Burg} and k_{nom} than between k_{Vand} and k_{nom} (Fig. 4B). Though k values are rarely stated explicitly in sap flow studies, wood scientists have reported similarly low values of k for green wood (Maku 1954, Steinhagen 1977, Herrington 1969, Simpson and TenWolde 1999). The discrepancy between calculated k and k_{nom} may be due to the high m_c of conifer sapwood, which exceeds the range of m_c considered in recent studies (e.g., Vergeynst et al. 2014, Vandegehuchte and Steppe 2012). Our measured m_c and ρ_b agreed well with values published for the studied species (Simpson and TenWolde 1999, Markstrom and Hann 1972, Chave et al. 2009, Zanne et al. 2009), suggesting that measurement errors (e.g., use of core dimensions rather than water displacement to estimate core volume) likely exerted minimal influence on our findings.

Following the reasoning of Marshall (1958), V_s/V_h should be greater than 1; however, because V_s/V_h varies positively with m_c , the combinations of m_c and ρ_b for which V_s/V_h was greater than 1 were associated with declines in calculated k (Fig. 4C); hence, m_c exerts opposing effects through the two steps (I and IV in Fig. 1), with a net positive effect (Fig. 4D) on the process of converting V_h (with k_{nom}) to V_s . Because ρ_b influences sap flow estimation both through its relationship with m_c (Fig. 2) and independently (Eqns. 2 and 3), the net effect of m_c differed slightly among species (Fig. 4).

Though variability in m_c and ρ_b clearly influenced the estimation of V_s in the five conifers we studied, the choice of method for specifying k (use of k_{nom} or calculation of k_{Burg} or k_{Vand}) constituted a larger, and potentially more problematic, source of uncertainty. With both calculation methods, estimates of k based on our m_c and ρ_b measurements deviated systematically from k_{nom} (Fig. 2A-B). However, the magnitude and pattern of this deviation differed between the methods. Our simulation indicated that k_{Vand} equaled k_{nom} at greater m_c than did k_{Burg} (i.e., x -intercepts of curves in Fig. 4B) and that changes in m_c resulted in smaller changes in k_{Vand} than in k_{Burg} (slope of curves in Fig. 4A). Estimates of k from the two methods converged only as m_c approached 0 kg kg^{-1} . The net scaling effect, N , reduced the intraspecific variation in simulated velocities in a manner that depended on whether k_{Vand} or k_{Burg} was used (Fig. 5), indicating that the systematic bias associated with the choice of calculation method is likely of greater importance than core-to-core variation in sapwood properties.

Specification of a value for k in HRM-based studies remains a matter of the researcher's best judgment, and few practitioners explicitly state which approach they used or publish the resultant values. Thermodynamic principles underlie the calculations of k_{Burg} and k_{Vand} , but both methods assume that green wood can be modeled as a linear mixture of water and dry wood; future experimental analysis may prove useful in testing that assumption. The method of Vandegehuchte and Steppe (2012) accounts for additional physical complexity by separately considering the thermal conductivities of bound and free water. Both methods have performed well in independent assessments of sap flow rates: Burgess et al. (2001) validated k_{Burg} by comparing HRM-based results against those from a different heat-pulse method that does not require k and against gravimetric water loss. Vandegehuchte and Steppe (2012) found that sap flow scaled with k_{Vand} was closer to gravimetrically determined rates than when k_{Burg} was

used in scaling. Hence, current evidence supports the use of k_{Vand} rather than k_{Burg} or k_{nom} . To further improve confidence in k estimates, gravimetric techniques (or sap flow methods that do not require k) should be used to validate HRM measurements in trees representing a wider range of m_c and ρ_b than previous studies have considered. As Marshall (1958) acknowledged, k may also be estimated on the basis of the temperature rise curve following the heat pulse. This approach, which is becoming increasingly feasible in the field as data storage capacity improves, was recently extended using a Bayesian inversion technique (Chen et al. 2012) and warrants further exploration.

4.2. *Sampling of sapwood traits at different scales induces major uncertainty in Q .*

Because logistical considerations often preclude direct measurement of sapwood traits in trees instrumented with sap flow probes, the auxiliary factors required to estimate Q are often established for co-occurring trees. In the case of A_s , true values may be unavailable altogether, leading to the use of R_s or a DBH-based regression to estimate A_s in sample trees. We resampled a nested dataset of m_c , ρ_b , and R_s in Douglas-fir to assess how cross-scale variability in these traits may contribute to uncertainty in Q .

Cross-scale variation in m_c and ρ_b exhibited a range of effects on the scaling process (N). Within several trees, variation in these traits had negligible effects on determination of N ; that is, each core sample yielded a similar value of N . On the other hand, variation within other trees suggested that the use of one core rather than another could lead to values of N that differed by up to 0.137, implying an equal error in Q . At each scale, the consequences of this variability were generally more severe when k_{Vand} was used rather than k_{Burg} (Fig. 6). Though this may appear to contradict the lesser sensitivity of k_{Vand} to variability in m_c (Fig. 4A), the

phenomenon evident in Figure 6 is likely a function of how the two methods behave in response to the joint variation of m_c and ρ_b . This bivariate sensitivity may be more easily conceptualized by comparing how the thermal diffusivity coefficient isolines are arranged in m_c - ρ_b space (Fig. 2A-B); the k_{Vand}/k_{nom} isolines follow a trajectory that differs from the sapwood samples more sharply than do the k_{Burg}/k_{nom} isolines. As with the simulation, these findings highlight how a methodological question (use of k_{Vand} or k_{Burg}) mediates the relative significance of error in m_c and ρ_b for uncertainty in sap flow calculations. The use of m_c and ρ_b values from a single core as surrogates for another part of the same tree or for a different tree in the same plot, in the same site, or at a different site may be of greater concern when using k_{Vand} rather than k_{Burg} , at least for species exhibiting a similar trait distribution to the conifers in our study.

Sapwood area, A_s , has a direct effect on sap flow estimation, as it is the area across which measurements of V_s are integrated to obtain Q . Thus, our finding that A_s as estimated from R_s measured on a single core could differ from a circumferential four-core average A_s by as much as 40% (Fig. 7A) has serious implications for uncertainty in Q . Similarly, regression-based predictions of A_s as a function of DBH may differ substantially from A_s as estimated from R_s measured in a specific tree. When A_s is estimated on the basis of a regression or a single R_s measurement and then used to integrate V_s , the reported error in Q will be unrealistically small unless the uncertainty in A_s is retained throughout the scaling procedure.

4.3. Reducing error in, Q

Uncertainty in Q arises from error in V_s , A_s , and the integration of V_s across A_s . In turn, estimation of V_s is sensitive to the specification of sapwood thermal diffusivity (k_{nom} , k_{Burg} , or k_{Vand}) and variability in the data that are the basis for that estimation (m_c and ρ_b); probe

misalignment (Bleby et al. 2004) and xylem wounding (Vandegehuchte and Steppe 2013, Moore et al. 2010) introduce further uncertainty in V_s . Our results suggest that the joint variability of m_c and ρ_b affects calculations of V_s in a manner inconsistent with the theoretical arguments found in the literature. Specifically, though Marshall (1958) argued that V_s should exceed V_h , we found that to be possible (based on Eqn. 3) only for combinations of m_c and ρ_b that would yield values of calculated k much lower than k_{nom} (Fig. 2, Fig. 4C). However, because the change in m_c across individuals was associated with a corresponding change in ρ_b , the scaling coefficients k_{Burg}/k_{nom} , k_{Vand}/k_{nom} , and V_s/V_h varied less within a species than either of the variables from which they are calculated. Though variation in m_c and ρ_b at different sampling scales can contribute relative error greater than 0.1 to the scaling procedure (Fig. 6) and should be reported as part of the error in Q , how to determine k constitutes a systematic source of uncertainty demanding additional inquiry and independent validation efforts. In addition, errors in the estimation of A_s (e.g., due to departure from radial symmetry; Hatton et al. 1992) and in the integration of V_s across A_s (Alvarado-Barrientos et al. 2013, Kume et al. 2012) can have a substantial effect on variability in Q estimates, yet such errors are routinely omitted from the expression of uncertainty in Q . We emphasize that incorporation of these various sources of error into the stated uncertainty of sap flow rates will more realistically represent the accuracy of existing methods while catalyzing efforts to further improve confidence in auxiliary factors.

4.4. Implications for broader level inferences

Recognizing the random error and systematic uncertainty implicit in the estimation of Q may affect the conclusions drawn from statistical tests. We found significant differences in Q between co-occurring species more often when representing the Q values of each tree as a distribution

rather than as a point estimate. The detection of a difference was still a relatively infrequent occurrence (i.e., 1-36% of cases for Engelmann spruce and western larch) in the distributional approach, which was likely the result of sampling from opposite tails of the respective distributions. For instance, values of Q will occasionally be drawn from the upper tails of the Douglas-fir distributions and the lower tails of the Engelmann spruce distributions, yielding a significant difference in only a small fraction of iterations. While the incorporation of uncertainty in Q into analyses may have contrasting effects (e.g., increase or reduction of the standard error of species-mean Q) depending on the shape of the distribution of Q for each tree, inferences based on sap flow-scaled Q will be made more reliable and consistent if systematic handling of uncertainty becomes common practice.

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Table 1

Species	<i>n</i>	Range of ρ_b (kg m ⁻³)	<i>m</i>	<i>b</i>	Adj. R ²	<i>p</i> -value	Standard deviation of residuals	Range of daytime <i>V_h</i> (cm h ⁻¹)
DF	34	378-552	-0.0048*	4.1*	0.39	<0.0001	0.27	-1.8-21.3
ES	9	331-546	-0.0081*	5.5*	0.64	0.006	0.34	-1.1-19.4
PP	6	393-496	-0.0059	4.5*	0.37	0.1	0.20	-0.30-13.7
SF	9	333-505	-0.0042	3.6*	0.06	0.3	0.42	-2.2-6.3
WL	10	399-570	-0.0064*	4.7*	0.87	<0.0001	0.16	-2.4-41.9

Table 1. Species-level ranges of sapwood density and heat-pulse velocity, with coefficients from the regression of sapwood water content against sapwood density. *m_c* = sapwood water content (kg kg⁻¹), *ρ_b* = sapwood density (kg m⁻³), and *V_h* = heat-pulse velocity (cm s⁻¹) calculated with nominal thermal diffusivity. *m_c* and *ρ_b* are reported for core samples removed from a radial depth of 0-2 cm. In the simulation, *ρ_b* was sampled from a uniform distribution defined by the range observed in each species. *m_c* was then predicted using the regressions, and an error term was added to each predicted value by sampling from a normal distribution with a standard deviation equal to the standard deviation of the residuals. Reported *V_h* values correspond to the average velocities from 9:00 to 18:00 h (averaged per day per individual tree). DF = Douglas-fir, ES = Engelmann spruce, PP = ponderosa pine, SF = subalpine fir, WL = western larch.
*Coefficient *p*-value < 0.05.

2-column figure

Figure1

Figure 1. Conceptual illustration of the calculation of whole-tree sap flow (Q). Using heat-ratio measurements to estimate Q or mean sap flux density (J) requires multiple types of data, each of which may contribute uncertainty to the overall estimate of Q or J . Spatiotemporal variability of auxiliary data sources, sampling effects, and methodological decisions impart random and systematic errors to the calculation process. Sapwood water content (m_c) and density (ρ_b) enter the procedure in the calculation of theoretical thermal diffusivity (k_{Burg} or k_{Vand} ; Step I) and in the conversion of heat-pulse velocity (V_h) to sap velocity (V_s ; Step II). The directional effect of each step (as theorized in the literature) is denoted by + or -.

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Figure 2. Measured sapwood water content (m_c) and density (ρ_b) from core samples overlaid on isolines of thermal diffusivity and sap velocity coefficients. Isolines were generated by solving the equations for thermal diffusivity (k) and sap velocity (V_s) for the values of m_c that would yield the same values of k or V_s across a range of ρ_b . **A.** Isolines of $k_{\text{Burg}}/k_{\text{nom}}$ (proportion of theoretical thermal diffusivity calculated following Burgess et al. (2001) to nominal thermal diffusivity, $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$). **B.** Isolines of $k_{\text{Vand}}/k_{\text{nom}}$ (proportion of theoretical thermal diffusivity calculated following Vandegehuchte and Steppe (2012) to nominal thermal diffusivity). **C.** Isolines of V_s/V_h (proportion of sap to heat-pulse velocities). DF = Douglas-fir, ES = Engelmann spruce, PP = ponderosa pine, SF = subalpine fir, WL = western larch.

2-column figure

Figure3

Figure 3. Sapwood depth (R_s , cm, panel A) and area (A_s , cm^2 , panel B) against diameter at breast height (DBH, cm) for each species. A_s was estimated on the basis of R_s , DBH, and bark depth using Equation 3. Each point represents the mean of two measurements of R_s per individual. DF = Douglas-fir, ES = Engelmann spruce, PP = ponderosa pine, SF = subalpine fir, WL = western larch. Regression of R_s on DBH for each species (p-value, adjusted R^2): DF: 0.007, 0.16; ES: 0.3, 0.04; PP: 0.02, 0.47; SF: 0.1, 0.18; WL: 0.2, 0.15. Regression of A_s on DBH: DF: <0.0001, 0.67; ES: 0.0005, 0.78; PP: <0.0001, 0.98; SF: 0.002, 0.67; WL: 0.003, 0.65.

1-column figure

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Figure 4. Sap flow calculation coefficients and errors for variable sets simulated on the basis of sapwood water content (m_c) and density (ρ_b) measurements in each species. **A.** Theoretical thermal diffusivity (k_{theo} , a function of m_c and ρ_b) calculated according to Burgess et al. (2001; k_{Burg}) and Vandegehuchte and Steppe (2012; k_{Vand}). **B.** Relative error in sap velocity (V_s) as calculated with nominal thermal diffusivity (k_{nom} , $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$; Marshall 1958) across a range of m_c . Relative error is the difference between V_s calculated with k_{nom} and k_{theo} divided by V_s calculated with k_{theo} . **C.** Coefficients k_{theo}/k_{nom} and V_s/V_h . **D.** The net effect (N) of water content and density on the conversion of heat-pulse velocity (V_h) calculated with k_{nom} to V_s . N is the product of k_{theo}/k_{nom} and V_s/V_h .

2-column figure

Figure 5. Simulated distributions of heat-pulse and sap velocities (V_h and V_s) in each species. The distributions of V_h (left panel) were generated by averaging recorded V_h rates over 9:00 to 18:00 h for each tree on each day of the study period and then resampling those daytime averages. V_h was converted to V_s using simulated sapwood water content (m_c) and density (ρ_b) and the methods of Burgess et al. (2001, middle panel) and Vandegehuchte and Steppe (2012, right panel) to calculate sapwood thermal diffusivity (k).

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Figure 6. Relative error in the net effect of sapwood water content (m_c) and density (ρ_b) incurred by substituting measurements obtained at different scales for the values of m_c and ρ_b in a particular core. Errors were obtained by resampling a dataset of m_c and ρ_b in Douglas-fir, calculating the difference in N between a reference core and a second core drawn from a different scale, and dividing that difference by N in the reference core. Relative errors were then averaged according to the scale from which the second core was drawn.

1-column figure

Figure 7. Relative error in Douglas-fir sapwood area (A_s) as estimated on the basis of sapwood depth (R_s), diameter at breast height (DBH), and bark thickness. **A.** Within-tree variability: error incurred in A_s (relative to the mean of A_s calculated from four measurements of R_s) in relation to the number of measurements used. The minimum and maximum relative errors in A_s due to use of <4 sapwood cores are represented for each tree by a translucent area. Error bars indicate median over- and underestimation of A_s per number of cores in the subset. **B.** Among-tree variability: error incurred in A_s (relative to the mean of A_s calculated from two measurements of R_s per tree) when A_s is predicted on the basis of DBH using a species-specific linear regression.

2-column figure

Figure 8. Resampling-based estimation of whole-tree water use (Q) coupled with iterative estimation of differences in Q between co-occurring species and in Douglas-fir across sites. Top plot: estimates of Q obtained for a single Douglas-fir; vertical lines indicate point estimates of Q calculated with k_{nom} and species-mean values of sapwood water content and density (m_c and ρ_b), whereas the distributions of Q were generated using either k_{Burg} (solid curves) or k_{Vand} (dashed curves) and species-specific distributions of m_c and ρ_b . Bottom plot: point estimates and distributions of Tukey's Honestly Significant Difference between co-occurring Douglas-fir and ponderosa pine trees.