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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.

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

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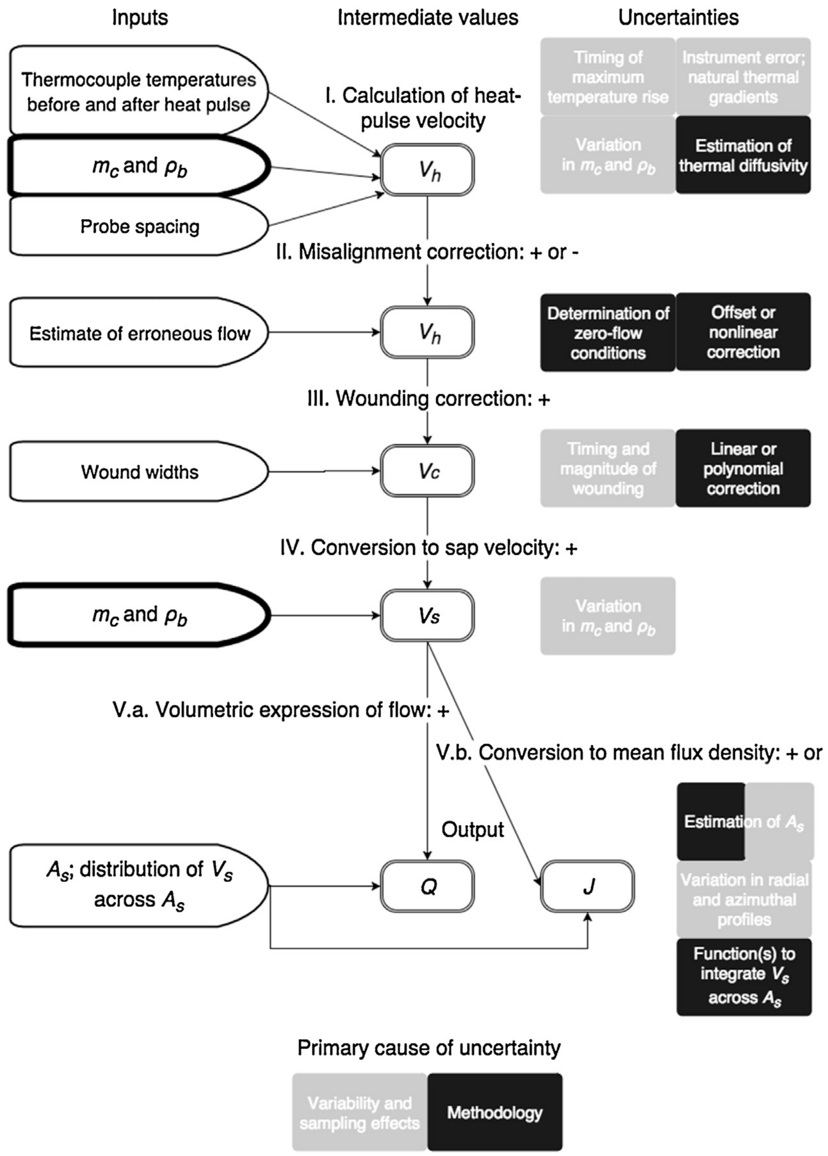

Fig. 1. Conceptual illustration of the calculation of whole-tree sap flow (Q). Using heat-ratio measurements to estimate Q or mean sap flux density (J) requires multiple types of data, each of which may contribute uncertainty to the overall estimate of Q or J. Spatiotemporal variability of auxiliary 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 −.

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

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

where x is heater-to-thermocouple spacing in the axial direction (cm), k is sapwood thermal diffusivity (cm^2 s^{-1}), and v_u and v_d are the respective up- and downstream temperature rises (°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 2.5×10^{-3} cm^2 s^{-1} (hereafter k_nom), which is intermediate between thermal diffusivities of water (1.4×10^{-3} cm^2 s^{-1}) and of dry wood (4.0×10^{-3} cm^2 s^{-1}), as originally noted by Marshall