

CONIFER TRANSPIRATION IN A MONTANE WATERSHED:  
ENVIRONMENTAL CONTROLS AND METHODOLOGICAL  
UNCERTAINTIES

by

Nathaniel Thomas Looker

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY  
Bozeman, Montana

July 2015

©COPYRIGHT

by

Nathaniel Thomas Looker

2015

All Rights Reserved

## ACKNOWLEDGEMENTS

The following work would not have been possible without the support and encouragement of my advisor, Jia Hu, and my committee members, Ben Poulter and Anna Sala. Their mentorship has been invaluable to my development as a researcher. I am also deeply indebted to my lab mates Justin Martin, Yuriko Yano, and Sarah Amish and our collaborators at the University of Montana, including Kelsey Jencso, Zach Hoylman, and Anna Bergstrom. The Department of Ecology staff was instrumental to my success as a graduate student; in particular, I thank Judy Van Andel, Joan Macdonald, and Meghan Heim for their unceasingly patient assistance.

Family and friends helped me hone my research ideas while keeping me in high spirits throughout my program. I extend heartfelt thanks to my parents, Joan and Dan, my sisters, Colleen and Maureen, and my grandmother, Ellen, as well as to my partner, Aspen. Many friends in the Department of Ecology and beyond made critical contributions to how I thought about and executed my project; in particular, I thank Jim Junker, Dan Bachen, Ryan Lamb and Rob Payn for their observations and suggestions.

This work was supported in part by the Montana Institute on Ecosystems and by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1049562.

## TABLE OF CONTENTS

|                                                                                |    |
|--------------------------------------------------------------------------------|----|
| 1. INTRODUCTION .....                                                          | 1  |
| References Cited .....                                                         | 4  |
| 2. TOPOGRAPHIC MEDIATION OF SAP FLOW<br>DYNAMICS IN A FORESTED WATERSHED ..... | 6  |
| Contribution of Author and Co-Authors .....                                    | 6  |
| Manuscript Information Page .....                                              | 7  |
| Introduction .....                                                             | 8  |
| Materials and Methods .....                                                    | 11 |
| Study Site .....                                                               | 11 |
| Hydrometeorological Measurements .....                                         | 12 |
| Sap Flow Measurements .....                                                    | 13 |
| Stem Water Potential Measurements .....                                        | 15 |
| Analyses .....                                                                 | 16 |
| Results .....                                                                  | 18 |
| Hydrometeorology .....                                                         | 18 |
| Sap Flow .....                                                                 | 19 |
| Stem Water Potential .....                                                     | 20 |
| Analyses .....                                                                 | 20 |
| Discussion .....                                                               | 22 |
| Hillslope-scale Heterogeneity in Plant Water Relations .....                   | 23 |
| Inferential Uncertainties .....                                                | 25 |
| Conclusion .....                                                               | 27 |
| Tables .....                                                                   | 29 |
| Figures .....                                                                  | 30 |
| References Cited .....                                                         | 37 |
| 3. UNCERTAINTY IN CONIFER TRANSPIRATION DUE TO<br>SAPWOOD TRAITS .....         | 43 |
| Contribution of Author and Co-Authors .....                                    | 43 |
| Manuscript Information Page .....                                              | 44 |
| Introduction .....                                                             | 45 |
| Scaling to Tree Transpiration with the HRM .....                               | 46 |
| Study Objectives .....                                                         | 49 |
| Materials and Methods .....                                                    | 50 |
| Study Site .....                                                               | 50 |

## TABLE OF CONTENTS – CONTINUED

|                                                                          |    |
|--------------------------------------------------------------------------|----|
| Field Measurements .....                                                 | 51 |
| Sap Flow .....                                                           | 51 |
| Scale Factors .....                                                      | 52 |
| Analyses .....                                                           | 54 |
| Objective 1 .....                                                        | 54 |
| Objective 2 .....                                                        | 58 |
| Results .....                                                            | 59 |
| Field Measurements .....                                                 | 59 |
| Analyses .....                                                           | 61 |
| Objective 1 .....                                                        | 61 |
| Objective 2 .....                                                        | 62 |
| Discussion .....                                                         | 63 |
| The Use of a Nominal Value for Thermal Diffusivity                       |    |
| Overestimates Heat-pulse Velocity and Whole-tree Water Use .....         | 64 |
| The Scale Factors $m_c$ , $\rho_b$ , and $R_s$ Exhibit Contrasting       |    |
| Patterns of Variability Within and Among Trees, Species, and Sites ..... | 66 |
| Reducing Error in Estimates of Whole-tree Transpiration, $Q$ .....       | 67 |
| Tables .....                                                             | 69 |
| Figures .....                                                            | 72 |
| References Cited .....                                                   | 79 |
| 4. CONCLUSION .....                                                      | 82 |
| REFERENCES CITED .....                                                   | 84 |

## LIST OF TABLES

| Table                                                                                                       | Page |
|-------------------------------------------------------------------------------------------------------------|------|
| 2.1. Outcome of three lag identification methodologies.....                                                 | 29   |
| 3.1. Parameters and variables used in the Monte Carlo<br>simulation of the sap flow scaling procedure. .... | 69   |
| 3.2. Estimates of coefficients and intercepts for<br>species-specific simple linear regressions. ....       | 70   |
| 3.3. Species-level mean values for sap flow and<br>scale factor measurements. ....                          | 71   |

## LIST OF FIGURES

| Figure                                                                                                          | Page |
|-----------------------------------------------------------------------------------------------------------------|------|
| 2.1. Map of Lubrecht Experimental Forest in western Montana .....                                               | 30   |
| 2.2. Diurnal relationship between vapor pressure deficit<br>and sap velocity on three different days .....      | 31   |
| 2.3. Hydrometeorological conditions at each hillslope site .....                                                | 32   |
| 2.4. Cumulative distributions of sap velocity .....                                                             | 32   |
| 2.5. Seasonal course of normalized sap velocity .....                                                           | 33   |
| 2.6. Example sap flow dynamics during wet-up events in August .....                                             | 33   |
| 2.7. Response of sap velocity to vapor pressure deficit<br>in contrasting topographic positions .....           | 34   |
| 2.8. Stem water potential in south-facing sites .....                                                           | 34   |
| 2.9. Adaptive dissimilarity index for sap velocity<br>and vapor pressure deficit .....                          | 35   |
| 2.10. Time course of parameter estimates for hyperbolic model .....                                             | 35   |
| 2.11. Soil moisture against model residuals .....                                                               | 36   |
| 3.1. Conceptual illustration of the scaling procedure .....                                                     | 72   |
| 3.2. Construction of the mean diurnal heat-pulse curve .....                                                    | 73   |
| 3.3. Sapwood core properties and scaling coefficient isolines .....                                             | 74   |
| 3.4. Theoretical thermal diffusivity for sampled cores .....                                                    | 75   |
| 3.5. Relative error in transpiration in relation to<br>sapwood water content from Monte Carlo simulations ..... | 76   |
| 3.6. Scaling coefficients for simulated trees .....                                                             | 77   |
| 3.7. Net effects of sapwood water content and density on scaling .....                                          | 77   |

## LIST OF FIGURES – CONTINUED

| Figure                                                                                                 | Page |
|--------------------------------------------------------------------------------------------------------|------|
| 3.8. Variance in sapwood water content, density, and depth<br>partitioned across sampling levels ..... | 78   |



## ABSTRACT

Transpiration, the evaporative loss of water from vegetation through stomata, is intertwined with biological, meteorological, and hydrologic processes from the scale of leaves to continents. Among the methods of estimating transpiration, thermometric sap flow sensors have gained favor due to their high temporal resolution and capacity to integrate across sub-canopy variability. Heterogeneity in growing conditions through space and time may contribute substantial uncertainty to sap flow-based inferences; hence, quantification of spatiotemporal variability in sap flow dynamics and plant physiological traits is required to improve confidence in transpiration estimates. In this study, I employ sap flow sensors to address the environmental sensitivity of water use dynamics in conifers growing in contrasting topographic positions (elevations, aspects, and hillslope positions) within a watershed; additionally, I explore how variability in sapwood traits may contribute to uncertainty in sap flow-based estimates of whole-tree transpiration. To these ends, I measured sap flow in 32 trees of 5 species throughout the 2014 growing season and estimated sapwood traits in those individuals and in co-occurring trees. I related sap flow dynamics to environmental variables (vapor pressure deficit and soil moisture) through lag analyses and nonlinear regression. A Monte Carlo-based simulation and mixed effects variance decomposition served to quantify the sensitivity of transpiration to variability in sapwood traits and the magnitude of that variability across ecological scales. The response of sap flow to vapor pressure deficit varied with species and across topographic positions, and sap flow dynamics diverged spatially as soil moisture declined during the summer. The simulation suggested that a common assumption (constant wood thermal diffusivity) could impart up to 100% overestimation of transpiration in trees with sapwood properties similar to those I observed. Taken together, these findings underscore the importance of sampling sap flow and sapwood traits at the spatiotemporal scale for which inferences are to be drawn.

## INTRODUCTION

Human interest in water use by woody plants, particularly forest trees, arose as early as the first century A.D. (Andréassian 2004). Changes in streamflow observed after land cover change (e.g., deforestation) generated anecdotal support for the uptake of water by vegetation; the same logic underlies the contemporary water balance approach, in which the difference between precipitation and streamflow provides an estimate of evapotranspiration (ET) at a given scale. In pursuit of more mechanistic estimations of ET, hydrologists, meteorologists, and plant ecophysiologicalists throughout the past century have developed methods that range in cost, assumptions, and scale suitability (e.g., leaf versus stand). Of these methods, thermometric estimation of sap flow has drawn substantial attention from field-based researchers across disciplines due to its low cost (relative to eddy covariance), minimal invasiveness (compared to lysimetry), and integration of intra-canopy variability (in contrast to leaf- or branch-level porometry; Wullschleger et al. 1998). Furthermore, modern datalogging capabilities allow for automated measurements of sap flow at sub-hourly scales, and the method facilitates observations in contexts where species diversity or topography induces surface heterogeneity.

Sap flow methods present a powerful tool for estimating water fluxes at the scale of a whole tree, plot, stand, or catchment, as well as a means of tracking how plants respond to changing resource availability or limitation (Burgess 2006). At the tree scale, sap flow data have illuminated the effects of tree aging and growth on water transport (Köstner et al. 2002) and provided insight into processes including hydraulic lift (Dawson

1996) and foliar water uptake (Gotsch et al. 2014). Stand-scale studies have investigated how transpiration varies with ecological succession (Ewers et al. 2011), management practices (Hernandez-Santana et al. 2011, Moore et al. 2004), and abiotic site conditions (Carter and White 2009, Hacke et al. 2000).

In water-limited environments, vegetation may indicate the occurrence and spatial distribution of hydrologic processes, such as subsurface flow (e.g., Hwang et al. 2012), while actively serving to partition water into vertical and horizontal fluxes (D’Odorico et al. 2010). Hence, in such environments, plant water relations embody both a cause (of the fate of water on the landscape or in the atmosphere) and a consequence (of upstream/upslope processes). Given the previously stated advantages of sap flow methods, these techniques have played a dominant role in the elucidation of plant hydraulic functioning in complex ecosystems.

This thesis represents an effort to better understand how landscape structure mediates the relationship between tree water use and environmental conditions. At the same time, through the two subsequent chapters, I have sought to identify how the complexities inherent to all biological systems may be manifested in tree hydraulic functioning and incorporate this perspective into my application of sap flow methods.

In the second chapter, I address the question of how individuals of five coniferous species growing in contrasting topographic positions use water throughout the growing season. After comparing sap flow dynamics among species and topographic positions, I relate observed patterns in sap flow to environmental drivers, namely vapor pressure deficit and soil moisture. The third chapter examines how variability in wood properties

within a watershed may contribute to uncertainty in sap flow-based transpiration estimates. In sum, the two complementary studies highlight the necessity of cautious sampling through time and space when sap flow methods are applied in a heterogeneous environment.

## REFERENCES CITED

- Andréassian, V (2004) Waters and Forests: From Historical Controversy to Scientific Debate. *J. Hydrol.* 291: 1–27.
- Burgess SSO (2006) Measuring transpiration responses to summer precipitation in a Mediterranean climate: a simple screening tool for identifying plant water-use strategies. *Physiol. Plantarum* 127:404–412.
- Carter JL, White DA (2009) Plasticity in the Huber value contributes to homeostasis in leaf water relations of a mallee Eucalypt with variation to groundwater depth. *Tree Physiol.* 29:1407–1418.
- Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the role of tree size and hydraulic lift. *Tree Physiol.* 16:263–272.
- D’Odorico P, Laio F, Porporato A, Ridolfi L, Rinaldo A, Rodriguez-Iturbe I (2010) Ecohydrology of Terrestrial Ecosystems. *BioScience*, 60(11):898-907.
- Ewers BE, Bond-Lamberty B, Mackay DS (2011) Consequences of stand age and species’ functional trait changes on ecosystem water use of forests. In "Size- and age-related changes in tree structure and function" eds. Rick Meinzer, Todd Dawson, Barb Lachenbruch. Springer, Dordrecht, 481-506.
- Gotsch SG, Asbjornsen H, Holwerda F, Goldsmith GR, Weintraub AE, Dawson TE (2014) Foggy days and dry nights determine crown-level water balance in a seasonal tropical montane cloud forest. *Plant Cell Environ.* doi:10.1111/pce.12151
- Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schäfer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia*, 124:495–505.
- Hwang T, Band LE, Vose JM, Tague C (2012) Ecosystem processes at the watershed scale: Hydrologic vegetation gradient as an indicator for lateral hydrologic connectivity of headwater catchments. *Water Resour. Res.* 48, doi:10.1029/2011wr011301.
- Hernandez-Santana V, Asbjornsen H, Sauer T, Isenhardt T, Schilling K, Schultz R (2011) Enhanced transpiration by riparian buffer trees in response to advection in a humid temperate agricultural landscape. *For. Ecol. Manag.* 261:1415–1427.

- Köstner B, Falge E, Tenhunen D (2002) Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. *Tree Physiol.* 22:567–574.
- Moore GW, Bond BJ, Jones JA, Phillips N, Meinzer FC (2004) Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon, USA. *Tree Physiol* 24:481–491.
- Wullschleger SD, Meinzer FC, Vertessy RA (1998) A review of whole-plant water use studies in trees. *Tree Physiol.* 18:499–512.

## CHAPTER TWO

### TOPOGRAPHIC MEDIATION OF SAP FLOW DYNAMICS IN A FORESTED WATERSHED

#### Contribution of Authors and Co-Authors

Manuscript in Chapter 2

Author: Nathaniel Thomas Looooker

Contributions: Conceived study design and analyses. Conducted field work and analyses. Drafted the manuscript.

Co-Author: Justin Martin

Contributions: Assisted with field work. Provided feedback on the manuscript.

Co-Author: Zachary Hoylman

Contributions: Assisted with field work. Executed mapping component of the study. Provided feedback on the manuscript.

Co-Author: Kelsey Jencso

Contributions: Contributed to conceptual framework of the project. Assisted with field work.

Co-Author: Jia Hu

Contributions: Contributed to conceptual framework of the project. Conceived study design and analyses. Assisted with field work. Revised the manuscript.

Manuscript Information Page

Nathaniel Looker, Justin Martin, Zachary Hoylman, Kelsey Jencso, Jia Hu  
Ecohydrology

Status of Manuscript:

☒ Prepared for submission to a peer-reviewed journal

☐ Officially submitted to a peer-review journal

☐ Accepted by a peer-reviewed journal

☐ Published in a peer-reviewed journal

Published by John Wiley & Sons, Ltd.



## TOPOGRAPHIC MEDIATION OF SAP FLOW DYNAMICS IN A FORESTED WATERSHED

### Introduction

Plants release water to the atmosphere through transpiration as a tradeoff with carbon uptake. Because excessive water loss can result in physiological harm (e.g., turgor loss) or structural damage (cavitation in the hydraulic pathway), plants may restrict transpiration by reducing stomatal conductance,  $g_s$ , during brief or prolonged conditions of water deficit (Irvine et al. 1998). Optimality-based theories of stomatal behavior (Cowan and Farquhar 1977, Prentice et al. 2014) are supported by the tight coupling of primary productivity and transpiration in water-limited ecosystems (Noy-Meir 1973).

Landscape structure modulates water availability, which in turn shapes the capacity of vegetation to influence hydrology through transpiration. In landscapes with moderate to high relief, topography affects plant-level water balance through both belowground supply (soil moisture and groundwater; Tromp-van Meerveld and McDonnell 2006, Thompson et al. 2011) and aboveground demand (net radiation and vapor pressure deficit; Matyssek et al. 2009). Due to topographic mediation of the water balance, variables including elevation, aspect, and landform shape are often strongly associated with vegetation structure (Jenkins and Coop 2011), species composition (Iverson et al. 1997, Kopecky and Cizkova 2010), and productivity (Callaway et al. 1989, McNab 1989, 1993) at hillslope and catchment scales. In turn, vegetation may indicate the occurrence and spatial distribution of hydrologic processes, such as subsurface flow

(e.g., Hwang et al. 2012), while actively serving to partition water into vertical and horizontal fluxes (D'Odorico et al. 2010).

The rate and magnitude of the hydrologic functioning of vegetation depends, in part, on stand- and plant-level structural and physiological traits. Depending on site conditions, pertinent traits may include leaf area, root distribution, canopy height, stomatal sensitivity, and sapwood storage capacity, porosity, and conductive area (Bond et al. 2008). However, previous studies (e.g., Meinzer 2003, McDowell et al. 2002, Carter and White 2009) have provided considerable evidence of tradeoffs among plant hydraulic traits, suggesting that only a subset of traits, particularly leaf area index, canopy-averaged stomatal conductance,  $G_c$ , and/or rooting depth, may be required to efficiently predict the net hydrologic behavior of plant communities (Waring and Landsberg 2011, Mackay and Band 1997). Given that these traits are often sensitive to local water availability (Grier and Running 1977, Addington et al. 2006), distinguishing the reciprocal influences of vegetation and hydrology can pose methodological challenges.

Sap flow sensors allow for characterization of plant hydrologic behavior across species (Sala 2006), age and size classes (Ewers et al. 2011), and environmental conditions (Loustau and Granier 1993, Irvine et al. 1998). Whether interpreted as heat-pulse velocity, sap velocity, or sap flux density (Edwards et al. 1997), sap flow measurements are generally believed to be proportional to whole-tree transpiration,  $E_t$ , the plant-to-atmosphere efflux of water vapor, defined as the product of crown conductance,  $G_{ci}$ , and the leaf-to-atmosphere vapor pressure gradient,  $D_s$  (Loustau and Granier 1993). As  $G_{ci}$  integrates stomatal aperture and boundary layer aerodynamics, sap

flow measurements reflect physiological as well as abiotic conditions. Much research effort has been invested in the extraction of physiological signals from sap flow datasets. For instance, Oren et al. (1999) employed sap flow-derived estimates of  $G_{ci}$  (using vapor pressure deficit, VPD, as a surrogate for  $D_s$ ) alongside leaf-level measurements of  $g_s$  as support for the hypothesis that stomatal sensitivity is positively correlated with conductance rates at low VPD levels (1 kPa). Other studies (e.g., Phillips et al. 1997, Maherali and DeLucia 2001) have inferred the use of stored water (capacitance) from the lag between canopy transpiration or VPD and sap flow.

Clearly, sap flow methods can provide insight into plant physiological functioning. Such techniques have proven particularly useful in environments where topography or stand structure impede the scaling-up of leaf-level gas exchange measurements. However, in just such heterogeneous environments, biophysical conditions vary substantially through space and time, and the distinction of environmental signals from physiological responses will likely depend on how sap flow data are analyzed and interpreted. For example, the relationship between sap flow and environmental variables (e.g., VPD) can vary temporally within an individual tree, causing physiological inferences to be dependent on the timing of measurement. Furthermore, hysteresis and nonlinearity in stomatal responses to environmental perturbations, as well as nonstationarity and aperiodicity in longer-term sap flow dynamics, violate the assumptions of many commonly used statistical tests (Ford et al. 2005).

With consideration of the intrinsic complexities of sap flow data, I sought to address two objectives: 1) to characterize the sap flow dynamics of individuals of five western conifer species growing across topographic positions (elevations, aspects, and hillslope positions) and 2) to assess the contributions of environmental factors (VPD and soil moisture) to the topographic contrasts in sap flow dynamics.

## Materials and Methods

### Study Site

As part of a hillslope ecohydrology research program at Lubrecht Experimental Forest (LEF; 47° N, 113° W), we conducted our study in the 18-km<sup>2</sup> watershed of the North Fork of Elk Creek (Fig. 2.1). Soils in the North Fork watershed are primarily derived from granite, with some influence of Belt rock and limestone on the northern periphery of the catchment (Zhu 2000). Historically, snowfall has constituted nearly half the annual precipitation at LEF (Nimlos 1986). For my study, I selected one north- and one south-facing zero-order hillslope at 1400 m; due to the predominance of perennial streamflow at 1750 m, we chose first-order hillslopes at that elevation, again including one north- and one south-facing hillslope. Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) dominated the stands in all four selected hillslopes. Co-occurring species included ponderosa pine (*Pinus ponderosa*) and western larch (*Larix occidentalis*) at 1400 m and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) at 1750 m. The dominant trees were relatively uniform in age (70-100 years old) throughout our sites due to a history of logging at LEF.

### Hydrometeorological Measurements

In a canopy gap in the hollow of each hillslope, I installed an EM50 datalogger (Decagon Devices, Inc., Pullman, WA) equipped with a high-resolution rain gauge, a shielded temperature/relative humidity sensor, and three 5TE sensors to measure soil volumetric water content ( $\text{cm}^3 \text{ cm}^{-3}$ ) on the basis of the dielectric constant at 10, 30, and 50 cm depths. I also installed an EM50 datalogger on the adjacent west-facing slope (approximately 30 m above the hollow in each site) to record soil volumetric water content at the same depths as in the hollow. To account for the effects of soil texture and bulk density on the relationship between the dielectric constant and true volumetric water content, I calibrated the field measurements of volumetric water content using regressions of sensor readings against gravimetric water content determined in the laboratory for samples from each horizon (adjusted  $R^2=0.94$ ). Assuming each 5TE sensor effectively measured the 10 cm above and below its vertical position, volumetric water content was converted to depth of water (mm) at each topographic position by multiplying each time series of volumetric water content by 200 mm and summing across the horizons. Due to occasional saturation at 50 cm in the 1750-m hollows, I restricted the integration of volumetric water content to the upper 40 cm of soil.

Using the half-hourly measurements of air temperature and relative humidity, I calculated the evaporative demand of the atmosphere as the vapor pressure deficit, VPD (kPa):

$$\text{VPD} = e_{(T)} - e_{(T)} * \text{RH}/100, \quad (\text{Eqn. 1})$$

where  $e_{(T)}$  is the saturation vapor pressure at air temperature  $T$  (K) and RH (%) is relative humidity. Following Tetens (1930),  $e_{(T)}$  is calculated as

$$e_{(T)} = 0.6108 \exp[17.27T / (T+237.3)]. \quad (\text{Eqn. 2})$$

Given the nonlinearity of Eqn. 2, estimation of VPD over longer intervals (day or season) requires calculating  $e_T$  (and  $e_{(T)} \cdot \text{RH}/100$ ) using minimum and maximum values of  $T$  and RH and averaging the results prior to the use of Eqn. 1 (Allen et al. 1998). For this study, I defined the 2014 growing season as May 1 to October 31 due to missing sap flow data in April.

### Sap Flow Measurements

To characterize the dynamic response of plant water use to environmental conditions across topographic positions, I measured heat-pulse velocity,  $V_h$  ( $\text{cm h}^{-1}$ ), at half-hour intervals using heat-ratio method (HRM) sap flow sensors (Burgess et al. 2001). Sensors were constructed following Hu et al. (2010), and sapwood thermal diffusivity (required for the calculation of  $V_h$ ) was estimated according to Vandegehuchte and Steppe (2012). The proportionality of  $V_h$  to sap velocity,  $V_s$  ( $\text{cm h}^{-1}$ ), is expressed by Swanson (1983) 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 water and wood, respectively,  $\rho_s$  is the density of water, and  $m_c$  and  $\rho_b$  are the water content and density of sapwood. While some studies have noted temporal changes in  $m_c$  (López-Bernal et al. 2014), others have documented relative stability in  $m_c$  in the midst of soil moisture depletion (Beedlow et al. 2007), suggesting that within-tree variability in  $m_c$  may overshadow temporal dynamics

upon repeated sampling of sapwood. Thus, I assumed that measurements of  $V_h$  were proportional to whole-tree transpiration,  $E_t$ . The HRM design I used permitted measurement of  $V_h$  at two sapwood depths per each probe set. Because I was concerned with the temporal patterns of  $V_s$  rather than with the absolute volume of water transpired, this study focused on the time series of  $V_s$  at 2.0 cm into the sapwood of each tree. In each site, I installed HRM sensors in two dominant Douglas-fir individuals per hillslope position (hollow or adjacent slope), as well as in two individuals of either ponderosa pine, subalpine fir, Engelmann spruce, or western larch, depending on which species were present (i.e.,  $n=16$  for Douglas-fir and  $n=4$  for all others). Diameter-at-breast-height (DBH) ranged from 19 to 67.3 cm, with a median DBH of 34 cm. Each tree received one probe set on the east side of the trunk and one on the west; the probe set with fewer missing values in its time series was selected to represent each tree.

I prepared the  $V_h$  dataset for analysis as follows. To adjust for errors due to probe misalignment, I first identified periods from 12 to 5 am when VPD was low ( $<0.5$  kPa) and rain had occurred at multiple sites. Assuming negligible sap flow during these periods, I averaged the apparent  $V_h$  recorded for each tree across these intervals and then subtracted the averages from each observation for the corresponding tree. To compare species means in  $V_s$ , I converted each time series of  $V_h$  to  $V_s$  using Eqn. 3. Species-mean  $m_c$  and  $\rho_b$  were estimated from sapwood samples extracted from trees co-occurring with sap flow trees, with at least three replicate trees per species per landscape position; these values of  $m_c$  and  $\rho_b$  were then used in Eqn. 3. For days with a full set of observations

(48), I integrated half-hourly  $V_s$  over the day to obtain a value proportional to daily transpiration.

Given the fixed positioning of the HRM probes and inherent variability in sapwood depth within and among trees (and, hence, in the fraction of the sapwood represented by the measurements), I normalized each time series following Link et al. (2014). Normalization consisted of dividing each time series by the 99.5<sup>th</sup> percentile of the observations; I normalized the half-hourly measurements as well as the daily-integrated  $V_s$  time series. Thus, after excluding 2 trees with severe noise and missing values, I obtained 30 time series of both half-hourly and daily frequency, with the value at each time representing a proportion of the maximum  $V_s$  observed across the season for a particular probe.

#### Stem Water Potential Measurements

For independent evidence of topographic differences in plant water status, I measured predawn (1 hour before sunrise) and midday (12-1 pm) stem water potential,  $\psi$  (MPa), three times throughout the growing season (June, July, and August). I chose four individuals of Douglas-fir co-occurring with HRM-instrumented trees in both hollow and slope positions in the two south-facing sites (i.e.,  $n=16$ ). I also selected four ponderosa pine trees per hillslope position at the 1400 m site and four Engelmann spruce trees per position at the 1750 m site ( $n=8$  for each). For each tree, the tip of a sunlit branch was cut with a pole pruner at each sampling interval and inserted into a pressure chamber (Model 600, PMS Instrument Co., Albany, OR). I then recorded the pressure at which water emerged from the cut surface of the stem; this value, known as the balance pressure, is



widely interpreted as equal to, but opposite, the stem  $\psi$  (Scholander et al. 1965). Predawn and midday measurements of  $\psi$  were conducted on consecutive days for the two sites. I used the lme4 package (Bates et al. 2014) in R version 3.2.0 (R Core Team 2015) to fit a linear mixed effects model and assess the evidence for differences in  $\psi$  among topographic positions. I also used separate multiple linear regressions to estimate topographic differences in predawn and midday  $\psi$  for each month.

### Analyses

To better understand the environmental drivers of topographic patterns in sap flow dynamics, I analyzed sap flow dynamics through two complementary approaches, first by examining diurnal lags between VPD and  $V_s$  in a subset of trees and then by relating VPD and  $V_s$  across the growing season.

Cross-correlation analysis is widely applied to identify the temporal offset that yields the maximum correlation between two time series (Oren et al. 1998, Shinohara et al. 2013); however, the assumption of linearity underlying this method may be violated in sap flow applications. To assess how the choice of method may affect inference on lags (and possible interpretation of physiological traits), I compared cross-correlation analysis with two alternative methods of assessing diurnal lags between VPD and  $V_s$ : the adaptive dissimilarity index and the error of a nonlinear regression.

For the first analysis, I identified the temporal offset (lead or lag) that yielded the maximum cross-correlation between VPD and  $V_s$  for each day of the growing season, using the half-hourly time series of the four instrumented Douglas-fir trees at the 1750-m south-facing site. After observing that the highest cross-correlation generally fell within a

four-hour window, I used a subset of leads and lags ( $t \pm 120$  min) for alternative analyses on the same time series.

In the second analysis, I calculated the adaptive dissimilarity index using the TSclust package (Montero and Vilar 2014) in R. This index, developed by Chouakria-Douzal and Nagabhushan (2007) for automated classification of time series, integrates distance-based indices with a temporal correlation coefficient that estimates the similarity of the behavior of the two time series. The method permits weighting of the relative importance of time series values (distance) and behaviors (trends) in the determination of the overall dissimilarity of the observations. Distance between VPD and  $V_s$  time series was calculated via the Dynamic Time Warping algorithm, which is robust to nonlinearities and shifts in temporal offsets between time series. The lag that minimized that calculated index was identified each day.

For the third approach to lag diagnosis, I fit a hyperbolic model of the form  $V_s = a \text{ VPD} / (1 + b \text{ VPD})$ , similar to the representation of VPD in models of  $g_s$  (Lohammar et al. 1980, Link et al. 2014). Parameter  $a$  describes the maximum potential value of  $V_s$  at a given level of VPD, and parameter  $b$  establishes curvature in the relationship. The two parameters were estimated for each day using modFit function in the FME package (Soetaert and Petzoldt 2010) in R. For each day, the root mean square error (RMSE) was estimated for each parameter set and used as the criterion for identification of the optimal lag. In minimizing the RMSE, I assume that hysteresis (resulting in error about the regression curve; Fig. 2.2) is primarily due to lags rather than co-limitation by other environmental factors (Roddy et al. 2015). The performance of the three methods was

compared by calculating the proportion of days for which each method specified a leading relationship, a lagging relationship, or no temporal offset between VPD and  $V_s$ ; the proportions of days in each category were then averaged across the four trees.

I also used the adaptive dissimilarity index and the hyperbolic model to analyze seasonal sap flow dynamics. For each of the thirty normalized daily time series, I calculated the adaptive dissimilarity index between  $V_s$  and VPD, resulting in a set of thirty values indicating the relative difference between sap flow in each tree and VPD in the corresponding site. In contrast to a regression approach, this method requires no distributional assumptions or specifications of autoregressive error structures.

Finally, I estimated the parameters of the hyperbolic model for 30-day moving windows of the half-hourly measurements of VPD and normalized  $V_s$  in each tree. For each parameter set, I estimated model bias as the RMSE of predicted  $V_s$  over ten randomly selected days. To test possible midsummer soil moisture limitation of transpiration, I modeled growing season  $V_s$  with parameter estimates for the period of maximum soil moisture (days-of-year 150 to 180, May 30 – June 29) and plotted the residuals (summarized using the median residual for each day) against profile-integrated soil moisture.

## Results

### Hydrometeorology

Meteorological and soil moisture conditions exhibited similar patterns across the four hillslope sites but differed in terms of magnitude (Fig. 2.3). From May 1 to October

31, mean air temperature was lower at the 1750 m sites ( $10.1 \pm 0.07$  °C and  $9.9 \pm 0.07$  °C on north- and south-facing aspects) than at the 1400 m sites ( $12.2 \pm 0.08$  °C and  $12.5 \pm 0.08$  °C on north- and south-facing aspects). The timing of rain events was consistent across sites (Fig. 2.3A); cumulative precipitation varied across sites (212.4 mm at 1400 m south-facing site; 199.2 and 284.8 mm, respectively, at 1750 m north- and south-facing sites), but the apparent differences may have been due to gauge placement. Study period VPD as calculated with minimum and maximum T and RH ranged from 1.95 kPa (1750 m, south-facing site) to 2.56 kPa (1400 m, south-facing site), with maximum half-hour VPD as high as 5 kPa (1400 m, south-facing site). The behavior of VPD through time exhibited a similar pattern across sites (Fig. 2.3B), suggestive of thorough mixing of the lower atmosphere throughout the watershed. Mean soil moisture in the upper 40 cm ranged from  $13.8 \pm 0.5$  mm (slope at 1400 m, south-facing site) to  $45.1 \pm 0.9$  mm (hollow at 1750 m, north-facing site). Similar wet-up and dry-down behaviors were observed across sites (Fig. 2.3A).

### Sap Flow

The distribution of  $V_s$  varied within and across sites (Fig. 2.4). From May 1 to October 31, species-mean daytime  $V_s$  ranged from  $1.1 \pm 0.05$  cm h<sup>-1</sup> in Engelmann spruce to  $4.7 \pm 1.1$  cm h<sup>-1</sup> in western larch, with a maximum rate of 52.4 cm h<sup>-1</sup> observed in western larch. Profile plots of normalized daily  $V_s$  indicated that trees at the 1400 m sites reached their seasonal maximum rates earlier than trees at the 1750 m sites and that the lower elevation trees subsequently underwent a decline that was not as apparent at the higher elevation (Fig. 2.5). Normalized  $V_s$  approached (but did not fully achieve) its

early-season values at 1400 m in conjunction with the wet-up events identified in the soil moisture time series (Fig. 2.6). Trees within and among species exhibited variability both in terms of the shape of the sap flow response to VPD when soil moisture was plentiful and the rate with which the response curve changed shape as soil moisture declined (Fig. 2.7). The most extreme contrast was noted between the two south-facing sites, with intermediate conditions observed in the north-facing sites.

### Stem Water Potential

Topographic differences in  $\psi$  suggested spatial differentiation of plant water status by mid August (Fig. 2.8). After accounting for month and species, predawn  $\psi$  was estimated to be 0.21 MPa lower on the slope than in the hollow at the 1400 m south-facing site (95% confidence interval from 0.10 to 0.31 MPa lower); there was no evidence of a hollow-slope difference in predawn  $\psi$  at the 1750 m site (95% confidence interval from 0.08 MPa lower to 0.14 MPa greater on the slope than in the hollow). Douglas-fir generally exhibited the most negative values of both predawn and midday  $\psi$ , with less negative values at 1750 than at 1400 m. I found larger differences in  $\psi$  between elevation and hillslope positions than between co-occurring species.

### Analyses

My comparative analyses of diurnal and seasonal sap flow dynamics underscore the sensitivity of sap flow-based inferences to the analytical methods used and the time period examined. When I used cross-correlation analysis to identify temporal offsets between VPD and  $V_s$  in four sampled Douglas-fir trees, I found little evidence of a lag in

nearly half the days of the study period (Table 2.1); in contrast, the classification schemes based on the adaptive dissimilarity index and on the hyperbolic model RMSE identified lags of  $V_s$  with respect to VPD on approximately one third of days. Periods of consistent lags corresponded roughly to the soil moisture dry-down events (data not shown).

The adaptive dissimilarity indices revealed a tighter coupling of VPD and  $V_s$  at 1750 m than at 1400 m (Fig. 2.9); that is,  $V_s$  more closely tracked VPD (in terms of its behavior and normalized value) at the higher elevation sites than it did at the lower elevation sites. Douglas-fir generally resembled its co-occurring species in the index of  $V_s$ -VPD dissimilarity, with the exception of Engelmann spruce at the 1750 m south-facing site. The dissimilarity index did not systematically vary across hillslope positions, but greater spread in the index was evident at the 1400 m sites, suggesting hillslope-scale heterogeneity in soil moisture limitation.

The iterative fitting of the hyperbolic model indicated similar trends in parameters across trees (Fig. 2.10), though parameter estimates differed in magnitude across sites. At 1400 m,  $V_s$  increased most rapidly with VPD at the beginning of each dry-down period, with a subsequent flattening of the relationship with time (Fig. 2.7); this was reflected by a mid-season increase in estimates of  $b$  coupled with a decline in  $a$  at 1400 m.

Using the parameter estimates from days-of-year 150 to 180 and the full set of VPD measurements to predict daytime  $V_s$  across the growing season, the hyperbolic model systematically overestimated  $V_s$  (i.e., residuals became increasingly negative) with declining soil moisture for trees at 1400 m but not 1750 m (Fig. 2.11). Drawing parameter estimates from subsequent 30-day windows changed the proportion of over- to

underestimates (i.e., recentered the residuals with respect to the  $y$ -axis), but the shape of the relationship between residuals and soil moisture was consistent for each set of parameters. The decline in observed  $V_s$  relative to model predictions appeared to occur at different values of soil moisture for trees in each topographic position (on hollows and slopes at 1400 m north- and south-facing sites). While I did not attempt to model the threshold response of stomata to soil water deficits, these preliminary findings may be indicative of physiological acclimation to hillslope-scale variability in growing conditions.

### Discussion

Extensive theoretical and observational research underlies our current understanding of the hydrologic feedbacks between plants and their environment. In typical conditions, increases in VPD during the day and across the growing season lead to increases in  $E_t$ , which in turn contributes to a decline in  $g_s$  (Monteith 1995). Hydraulic and chemical signals from roots to leaves (Tardieu and Davies 1993) also exert control on stomatal behavior and, hence, modulate the response of  $E_t$  to atmospheric conditions. Through well-documented structural and physiological adjustments (e.g., McDowell et al. 2002), plants are capable of maintaining stable rates of liquid- and vapor-phase water flow despite intermittent water deficits (Addington et al. 2006).

Widely employed to estimate transpiration, sap flow sensors also serve as the basis for the estimation of plant physiological parameters of critical importance to the modeling of hydrologic and carbon fluxes. In particular, researchers have used sap flow

measurements to estimate canopy conductance (Oren et al. 1999, Ghimire et al. 2014), stomatal sensitivity (Oren et al. 1999, Gao et al. 2015), and slowly varying hydraulic traits, such as capacitance (Phillips et al. 2004). In this study, I assessed how sap flow dynamics of five conifer species varied across contrasting topographic positions, and I related observed differences in sap flow to environmental conditions. Though I did not explicitly link observed sap flow dynamics to specific plant traits, my findings indicate variation in water balance at a fine spatial scale ( $\sim 20$  m), which may, over multiyear time scales, impart a topographic structure to plant hydraulic traits.

#### Hillslope-scale Heterogeneity in Plant Water Relations

In agreement with other studies of conifers (e.g., Pataki et al. 2000, Link et al. 2014), I found that the dynamics of VPD explained much of the diurnal and seasonal variability in sap velocity,  $V_s$ , with soil moisture modulating that relationship at daily to seasonal time scales. On typical rain-free days,  $V_s$  increased with VPD in a curvilinear fashion (Fig. 2.7), often exhibiting hysteresis (i.e., different values of  $V_s$  at a given VPD depending on time of day). At both elevations (1400 and 1750 m) and on both north- and south-facing aspects, VPD reached its highest values in August (Fig. 2.3). The adaptive dissimilarity index-based analysis revealed that the time course of  $V_s$  in trees at 1750 m more closely tracked the seasonal development of VPD than was the case for trees at 1400 m (Fig. 2.9), indicative of greater (and/or more frequent) soil moisture limitation at 1400 m than at 1750 m. The effect of soil moisture on the VPD- $V_s$  relationship is apparent in the flattening of the diurnal response with declining soil moisture (Fig. 2.7).



My results also suggest a substantial degree of variability in  $V_s$  dynamics within hillslopes. Because I sought to explore environmental controls on  $V_s$  across a broader scale gradient of water availability, I could only allocate sensors to two individuals per species per hillslope position; notwithstanding low replication, observations of normalized daily sap flow (Fig. 2.5) and the parameter estimates for the hyperbolic model (Fig. 2.10) suggest that soil moisture limitation of  $V_s$  was more drastic on slopes than in the adjacent hollows. This pattern was consistent all four sites, though most pronounced at the 1400 m south-facing site. Possible mechanisms underlying this pattern may include spatial differences in infiltration rates (Thompson et al. 2010), soil or rooting depth (Tromp-van Meerveld and McDonnell 2006), and/or hydrologic connectivity (Jencso and McGlynn 2011).

My measurements of stem water potential (Fig. 2.8) provide additional evidence of hillslope-scale differentiation in plant water status. As the season progressed, both Douglas-fir and ponderosa pine exhibited more negative predawn  $\psi$  on the slope than in the adjacent hollow at the 1400 m south-facing site. However, in contrast to the sap flow time series, this hollow-slope distinction was not detected at 1750 m. Similarly, a relationship is evident in the plot of soil moisture against the residuals generated with early-season parameter estimates for the lower elevation trees, but that pattern is not apparent for the higher elevation trees (Fig. 2.11). In other words, declining soil moisture provides little insight into mid-season model bias for the trees at 1750 m, despite the observed decline in sap flow in trees growing on slopes at that elevation. The apparent lack of a difference in  $\psi$  between hillslope positions at 1750 m may be related to sample

size ( $n=4$  trees per species per hillslope position, 8 total) or poor representation of within-crown variability with the sampled branches. Alternatively, slope trees at the two elevations may in fact exhibit physiological differences in hydraulic conductance (Bond and Kavanagh 1999) or in the threshold at which soil moisture limits the response of  $V_s$  to VPD (Link et al. 2014). Such differences may also arise in response to site differences in soil texture (Hacke et al. 2000), nutrient status (Emanuel et al. 2007), air temperature, and/or growing season length.

### Inferential Uncertainties

Previous studies have emphasized the sensitivity of sap flow-scaled transpiration estimates to heterogeneity in environmental and stand conditions through space and time (Lorant et al. 2008, Adelman et al. 2008, Traver et al. 2010, Mackay et al. 2010, Ford et al. 2011, Angstrom et al. 2012). In this comparison of sap flow dynamics across topographic positions, I also observed fine spatial variability with implications for our capacity to predict how forest trees will respond to changing environmental conditions. Detection of this spatial variability depends on both the timing of sap flow measurements and the methods chosen for data analysis.

Due to equipment and labor costs, researchers often move sap flow instrumentation from tree to tree or from site to site (Carter Berry, pers. comm.). Extrapolation of water use dynamics beyond the period of measurement requires the assumption that sap flow will continue to respond to environmental conditions (or correlate with other trees or sites) in the same manner as during the period of measurement. In highly seasonal systems, where both plants and soil may exhibit

memory of past states, the period of measurement must be long enough to observe variable interactions and assess the importance antecedent conditions. Though the relationship between VPD and  $V_s$  is generally well understood, Figure 2.7 illustrates how the mediating effect of soil moisture differs over three successive periods of soil drying for some individuals (Douglas-fir in the hollow at 1400 m) but not others (ponderosa pine at the same position). Similarly, the parameter estimates for the hyperbolic model relating VPD and  $V_s$  were relatively constant through time for subalpine fir and Engelmann spruce but much more variable for all trees at 1400 m (Fig. 2.10). Hence, caution must be exercised when selecting the time period that will define the “representative” response of sap flow to environmental variables.

Furthermore, multiple features complicate the relationship of sap flow to environmental controls; given this complexity, different analyses may lead to contrasting conclusions. While my lag analysis served primarily as a methodological comparison, the finding that lagged behavior was underestimated by the cross-correlation analysis compared to the other two methods (Table 2.1) poses implications for the extraction of physiological information from sap flow data. For example, Maherali and DeLucia (2001) have argued that, if the canopy is assumed to lose water in synchrony with evaporative demand, a lag of sap flow behind VPD is evidence of the use of stored water. If I had used the cross-correlation approach to estimate the lag for each tree, I would likely have rejected a lagged relationship entirely. However, using two nonlinear approaches to identify the optimal lag for each day, I found evidence of extended periods over which sap flow did indeed lag VPD. Furthermore, all three methods indicated that

VPD lagged  $V_s$  on approximately half of the days in the study period; though this behavior may seem counterintuitive, it may arise when  $V_s$  responds directly to solar radiation (or another covariate) rather than to VPD. Given the thorough atmospheric mixing observed in coniferous forests, this finding is not likely a consequence of the siting of the meteorological station near the ground.

### Conclusion

Topography mediates water availability, which in turn affects the spatial distribution and productivity of vegetation (McNab 1993, Hwang et al. 2014), as well as the species composition (Kopecky and Cizkova 2010) and structure (Jenkins and Coop 2011) of the plant community. Transpiration, which represents a major pathway by which vegetation influences hydrology, varies in rate due to both physiological (Traver et al. 2010) and environmental variables (Tromp-van Meerveld and McDonnell 2006). The degree to which spatial patterns in transpiration are driven by these two sets of variables remains a question for future research. If, in fact, the physiological traits that mediate transpiration also vary with topography, antecedent physiological conditions (i.e., the distribution of hydraulic traits such as capacitance and stomatal sensitivity) may play a major role in determining sub-watershed feedbacks between hydrology and vegetation under changing environmental conditions (e.g., timing of precipitation). To more fully explain how topography modulates whole-plant hydraulic functioning, future efforts may uncover additional evidence through consideration of, for instance, sub-watershed variation in allometry (e.g., leaf area: sapwood area ratio) or the duration of non-limiting soil moisture conditions and possible effects on xylem hydraulic conductivity (e.g.,

through the proportion of earlywood to latewood). Subsequent sap flow-based approaches also promise to illuminate physiological variability, particularly with additional replicate observations in contrasting topographic positions and greater spatial resolution of soil moisture dynamics.

Tables

| Classification criterion     | Proportion of days per lag category |                 |                |
|------------------------------|-------------------------------------|-----------------|----------------|
|                              | No offset                           | VPD leads $V_s$ | VPD lags $V_s$ |
| Nonlinear model RMSE         | 0.27 (0.03)                         | 0.33 (0.09)     | 0.40 (0.06)    |
| Adaptive dissimilarity index | 0.09 (0.01)                         | 0.35 (0.07)     | 0.56 (0.06)    |
| Cross-correlation            | 0.47 (0.04)                         | 0.12 (0.05)     | 0.41 (0.05)    |

Table 2.1. Outcome of three lag identification methodologies. Using four Douglas-fir trees at the 1750-m south-facing site as an example, I identified the temporal offset between half-hourly measurements of vapor pressure deficit (VPD) and  $V_s$  that, for each individual day, optimized one of three criteria: minimization of the root mean square error (RMSE) from a hyperbolic model predicting  $V_s$  as a function of VPD, minimization of the adaptive dissimilarity index between VPD and  $V_s$ , or maximization of the cross-correlation between VPD and  $V_s$ . The proportions of days placed in each lead/lag category were averaged across the four example trees for each classification criterion; the standard error of the mean is presented in parentheses.

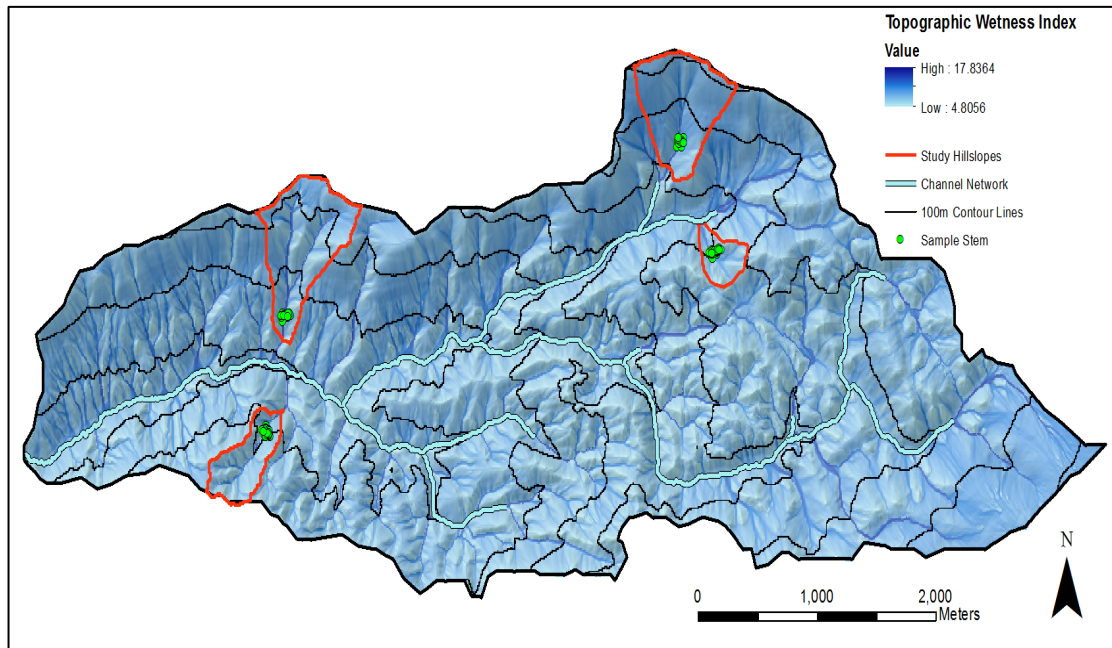
Figures

Figure 2.1. Map of Lubrecht Experimental Forest in western Montana. Elevation increases from west to east in the watershed of the North Fork of Elk Creek (outlined in black). The study was conducted in sites on north-facing and south-facing hillslopes (outlined in red and yellow, respectively).

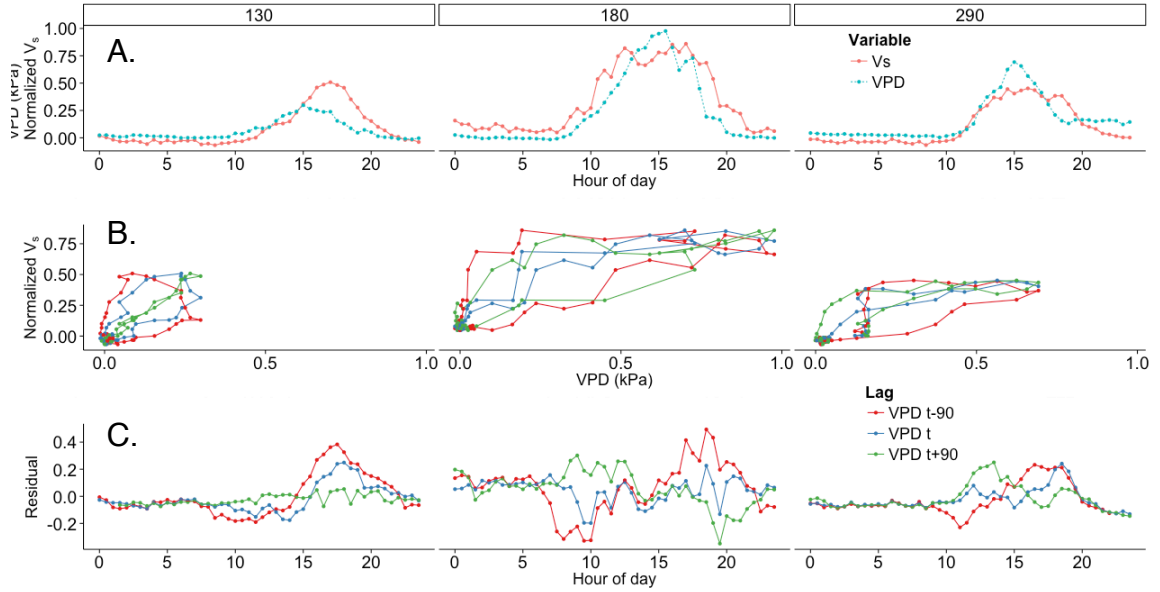


Figure 2.2. Illustration of the diurnal relationship between vapor pressure deficit, VPD (kPa), and normalized sap velocity,  $V_s$  (expressed as a proportion of maximum  $V_s$ ), in a single Douglas-fir tree on three different days (columns). A. Time series of VPD and normalized  $V_s$ . B. The effect of applying a temporal offset (lead or lag) on the hysteretic response of  $V_s$  to VPD. The separate lines indicate the relationship between  $V_s$  at time  $t$  with VPD at times  $t$ ,  $t - 90$  minutes (i.e., VPD leads  $V_s$ ), and  $t + 90$  minutes (i.e., VPD lags behind  $V_s$ ). C. Time series of residuals obtained from a hyperbolic model of the form  $V_s = a \text{ VPD} / (1 + b \text{ VPD})$ ; for this example, parameters  $a$  and  $b$  were estimated separately for each day and for VPD at times  $t$ ,  $t - 90$ , and  $t + 90$  using nonlinear least squares.



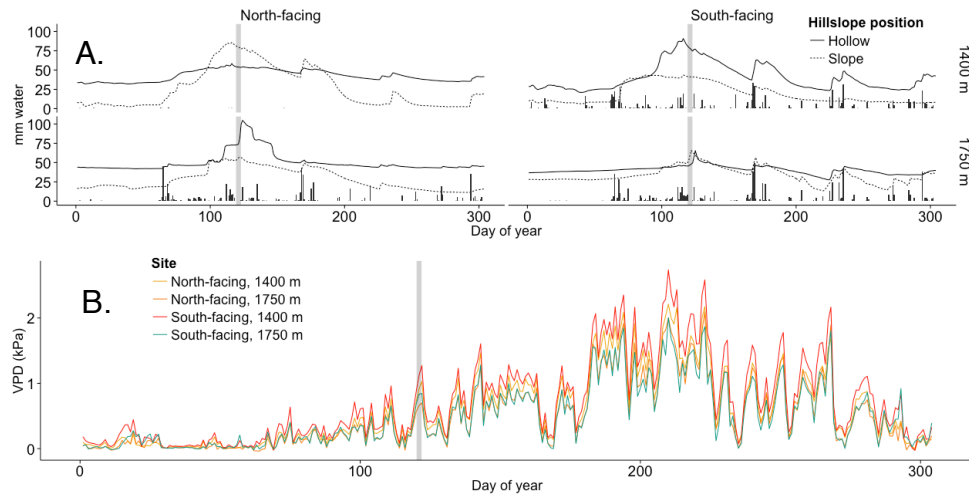


Figure 2.3. Hydrometeorological conditions at each hillslope site. A. Time course of soil moisture (mm, lines) and precipitation (mm, bars). Soil volumetric water content measurements at depths of 10 and 30 cm were integrated over a profile of 0–40 cm. Panels indicate north- and south-facing aspects and low (1400 m) and high (1750 m) elevations. Rainfall data are unavailable for the low-elevation north-facing site due to sensor malfunction. Gray bars indicate the beginning of the period for which sap flow data were available. B. Time course of vapor pressure deficit (kPa) in the hollow of each hillslope site.

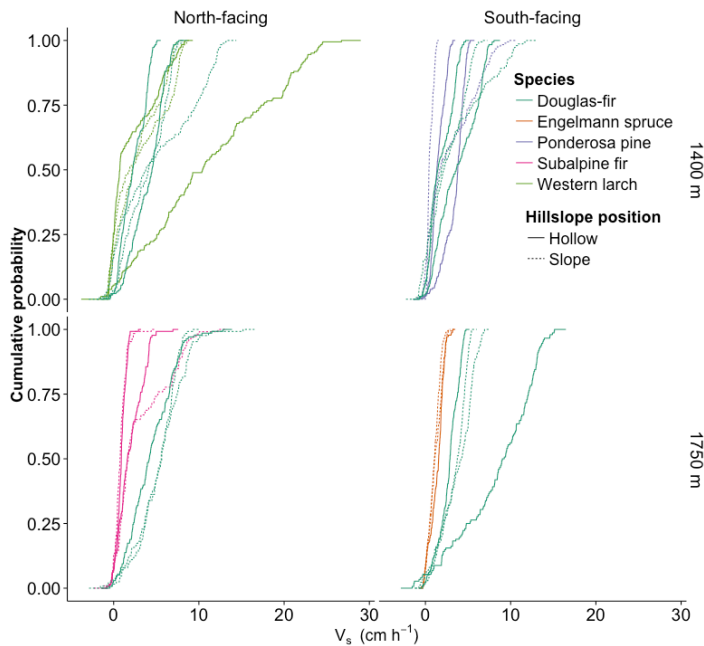


Figure 2.4. Empirical cumulative distributions of daytime (6 am to 8 pm) mean sap velocity,  $V_s$  (cm h<sup>-1</sup>), for each individual tree.

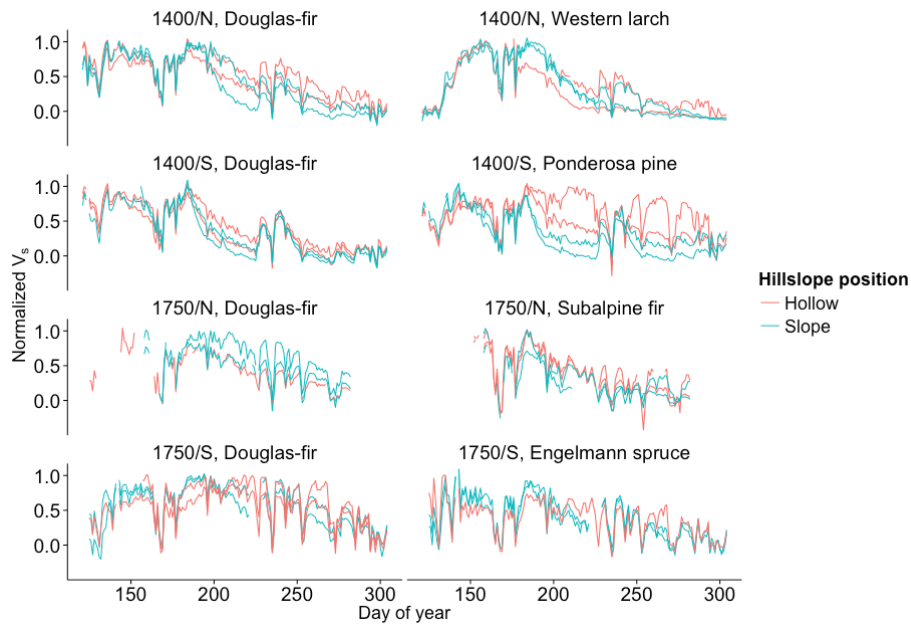


Figure 2.5. Normalized daily sap velocity,  $V_s$  (expressed as a proportion of probe-level maximum daily  $V_s$ ), for each tree. Sites are coded as Elevation/Aspect (i.e., 1750/S = 1750-m south-facing aspect).

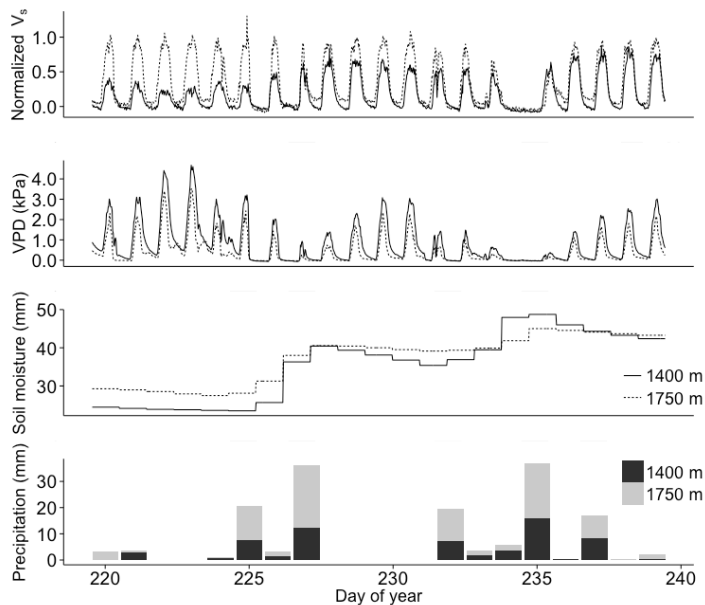


Figure 2.6. Normalized sap velocity,  $V_s$ , vapor pressure deficit, VPD (kPa), profile-integrated soil moisture (mm), and precipitation (mm) in the convergent hollows of the south-facing 1400- and 1750-m sites. One representative time series of  $V_s$  was selected from a Douglas-fir tree in the hollow of each site. Volumetric soil moisture data from the hollow of each site were integrated over depths from 0 to 40 cm.

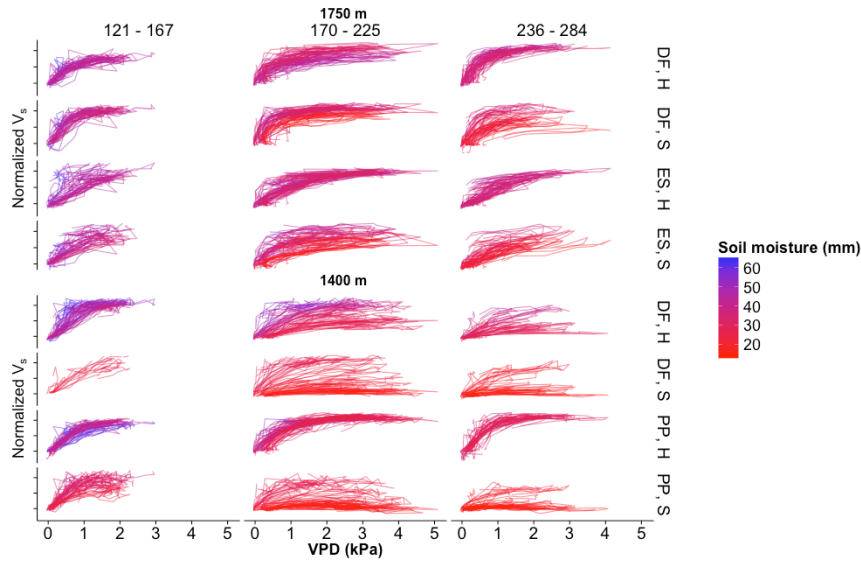


Figure 2.7. Response of normalized sap velocity,  $V_s$  (proportion of probe-level maximum hourly sap velocity), to vapor pressure deficit, VPD, in representative trees growing in contrasting topographic positions in 1750-m and 1400-m south-facing sites. Lines connect half-hourly measurements from each day in three periods of declining soil moisture (columns). DF=Douglas-fir, ES=Engelmann spruce, PP=ponderosa pine; H=hollow, S=slope.

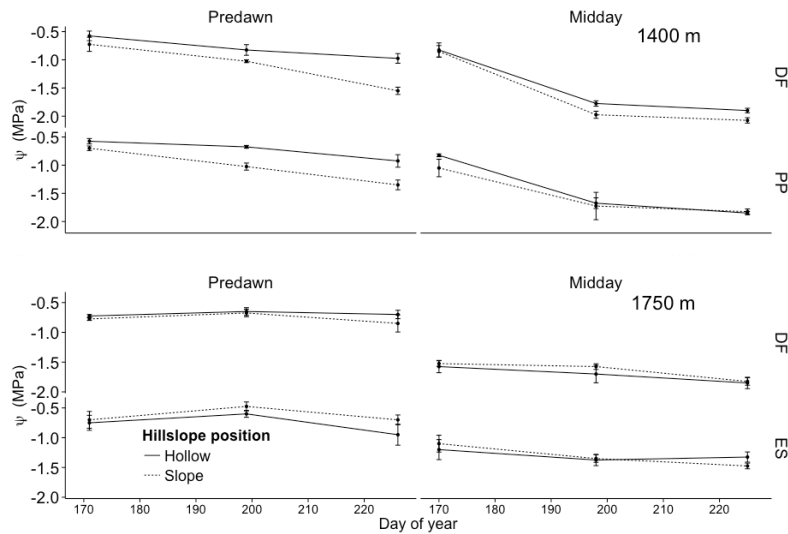


Figure 2.8. Stem water potential ( $\Psi$ ) as measured with a pressure bomb in branches of trees in south-facing sites. Each point represents species-mean  $\Psi$  at a specific topographic position and time of day, with bars indicating one standard error. DF=Douglas-fir, PP=ponderosa pine, ES=Engelmann spruce.

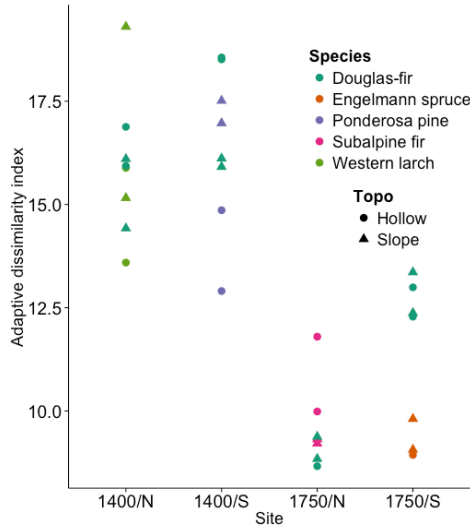


Figure 2.9. Adaptive dissimilarity index (Chouakria-Douzal and Nagabhushan 2007) between the time series of normalized daily vapor pressure deficit, VPD, and normalized daily sap velocity,  $V_s$ , of each tree. Higher values of the index indicate greater discrepancies in the value and/or dynamics of the two time series. Sites are coded as Elevation/Aspect (i.e., 1750/S = 1750 m, south-facing aspect).

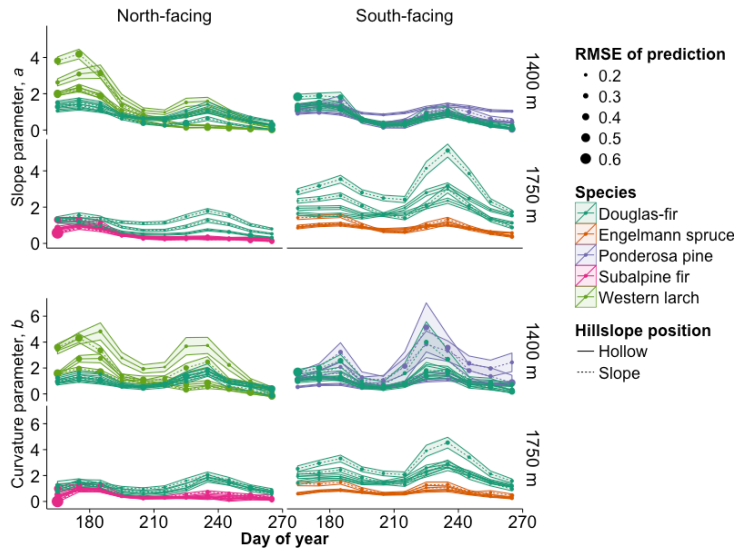


Figure 2.10. Time course of the slope parameter,  $a$ , and the curvature parameter,  $b$ , estimated for each tree over 30-day moving windows. A hyperbolic model of the form  $V_s = a \text{ VPD} / (1 + b \text{ VPD})$  was fit to half-hourly measurements of VPD and normalized  $V_s$  over each window using nonlinear regression. The performance of each pair of parameters, indicated by point size, was evaluated for each tree and time step as the root mean square error (RMSE) of predicted  $V_s$  over ten randomly selected days. Shading indicates the standard error of the parameter estimates.

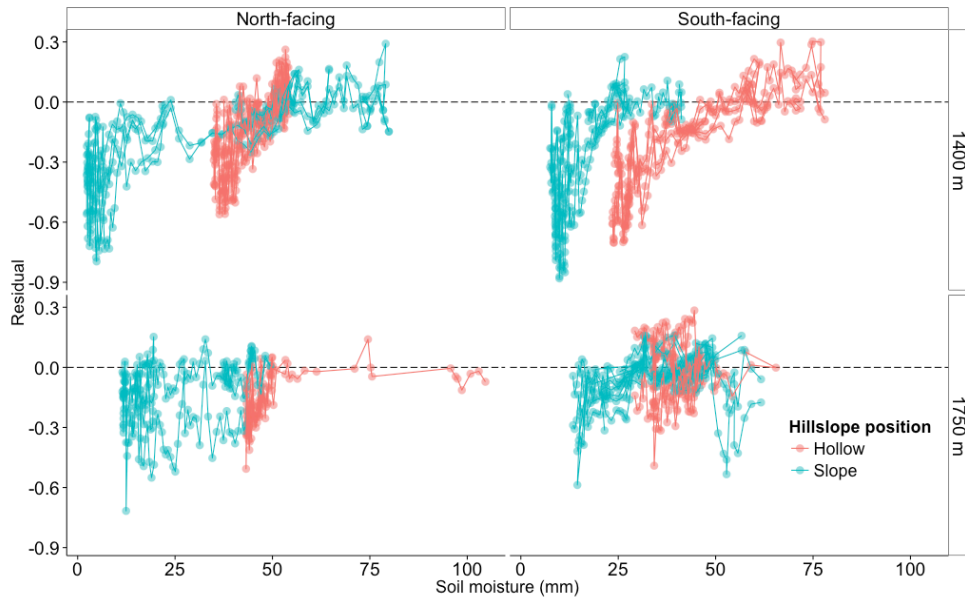


Figure 2.11. Soil moisture (mm) against residuals (observed  $V_s$  – predicted  $V_s$ ) obtained from a hyperbolic model of the form  $V_s = a \text{ VPD} / (1 + b \text{ VPD})$ . Parameters  $a$  and  $b$  were estimated for each individual tree over 30-day moving windows; here, residuals were generated using the parameter estimates for the period from day-of-year 150 to 180 (May 30 – June 29). Each point is the median value of the residuals for an individual day, and lines indicate the temporal order of days. Only residuals for Douglas-fir trees are displayed.

## REFERENCES CITED

- Addington RN, Donovan LA, Mitchell RJ, Vose JM, Pecot SD, Jack SB, Hacke UG, Sperry JS, Oren R (2006) Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats. *Plant Cell Environ.* 29:535–545
- Adelman JD, Ewers BE, Mackay DS (2008) Use of temporal patterns in vapor pressure deficit to explain spatial autocorrelation dynamics in tree transpiration. *Tree Physiol.* 28(4), 647–658.
- Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration. Guidelines for computing crop water requirements. FAO irrigation and drainage paper no. 56. FAO, Rome, 290 pp.
- Angstmann JL, Ewers BE, Kwon H (2012) Size-mediated tree transpiration along soil drainage gradients in boreal black spruce forest wildfire chronosequence. *Tree Physiol.* 32:599-611.
- Bates D, Maechler M, Bolker B, Walker S (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, <URL: <http://CRAN.R-project.org/package=lme4>>.
- Beedlow PA, Tingey DT, Waschmann RS, Phillips DL, Johnson MG (2007) Bole water content shows little seasonal variation in century-old Douglas-fir trees. *Tree Physiol.* 27:737–747.
- Bond BJ, Kavanagh KL (1999) Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. *Tree Physiol.* 19:503-510.
- Bond BJ, Meinzer FC, Brooks JR (2008) How trees influence the hydrological cycle in forest ecosystems, in *Hydroecology and Ecohydrology: Past, Present and Future*, eds. PJ Wood, DM Hannah, and JP Sadler. John Wiley & Sons, Ltd, Hoboken, NJ, USA, pp. 7-35.
- Burgess SSO, Adams M, Turner NC, Beverly CR, Ong CK, Khan AAH, Bleby TM (2001) An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiol.* 21:1157.
- Callaway RM, Clebsch EEC, White PS (1989) Predicting wood production by canopy trees in forest communities in the western Great Smoky Mountains. *Forest Science*, 35:338–348.

- Carter JL, White DA (2009) Plasticity in the Huber value contributes to homeostasis in leaf water relations of a mallee Eucalypt with variation to groundwater depth. *Tree Physiol.* 29: 1407–1418.
- Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment, in *Integration of Activity in the Higher Plant*, ed. DH Jennings. Cambridge University Press, Cambridge, UK, pp. 471–505.
- Chouakria-Douzal A, Nagabhushan PN (2007) Adaptive dissimilarity index for measuring time series proximity. *Adv. Data Anal. Classif.* 1(1): 5–21.
- D’Odorico P, Laio F, Porporato A, Ridolfi L, Rinaldo A, Rodriguez-Iturbe I (2010) Ecohydrology of Terrestrial Ecosystems. *BioScience*, 60(11):898-907.
- Edwards WRN, Becker P, Cermak J (1997) A unified nomenclature for sap flow measurements. *Tree Physiol.* 17:65–67.
- Emanuel RE, D’Odorico P, Epstein HE (2007) A dynamic soil water threshold for vegetation water stress derived from stomatal conductance models. *Water Resour. Res.*, 43, W03431, doi:10.1029/2005WR004831
- Ewers BE, Bon-Lamberty B, Mackay DS (2011) Consequences of stand age and species’ functional trait changes on ecosystem water use of forests, in *Size- and Age-related Changes in Tree Structure and Function*, eds. FC Meinzer, B Lachenbruch, TE Dawso. Springer, Dordrecht.
- Ford CR, Goranson CE, Mitchell RJ, Will RE, Teskey RO (2005) Modeling canopy transpiration using time series analysis: a case study illustrating the effect of soil moisture deficit on *Pinus taeda*. *Agric For. Meteorol.* 130:163–175.
- Ford CR, Hubbard RM, Vose JM (2011) Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. *Ecohydrology*, 4:183–195.
- Gao J, Zhao P, Shen W, Niu J, Zhu L, Ni G (2015) Biophysical limits to responses of water flux to vapor pressure deficit in seven tree species with contrasting land use regimes. *Agric. For. Meteorol.* 200:258-269.
- Ghimire CP, Lubczynski MW, Bruijnzeel LA, Chavarro-Rincón D (2014) Transpiration and canopy conductance of two contrasting forest types in the Lesser Himalaya of Central Nepal. *Agric. For. Meteorol.* 197:76–90.
- Grier CC, Running SW (1977) Leaf area of mature northwestern coniferous forests: relation to site water-balance. *Ecology* 58:893–899.

- Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schäfer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124, 495–505.
- Hu J, Moore DJP, Riveros-Iregui DA, Burns SP, Monson RK (2010) Modeling whole-tree carbon assimilation rate using observed transpiration rates and needle sugar carbon isotope ratios. *New Phytol.* 185:1000-1015.
- Hwang T, Band LE, Vose JM, Tague C (2012) Ecosystem processes at the watershed scale: Hydrologic vegetation gradient as an indicator for lateral hydrologic connectivity of headwater catchments. *Water Resour. Res.* 48, doi:10.1029/2011wr011301.
- Irvine J, Perks MP, Magnani F, Grace J (1998) The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiol.* 18(6):393–402
- Iverson LR, Dale ME, Scott CT, Prasad A (1997) A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.). *Landscape Ecol.* 12:331-348.
- Jencso KG, McGlynn BL (2011) Hierarchical controls on runoff generation: Topographically driven hydrologic connectivity, geology, and vegetation, *Water Resour. Res.*, 47, W11527, doi:10.1029/2011WR010666.
- Jenkins RB, Coops NC (2011) Landscape controls on structural variation in eucalypt vegetation communities: Woronora Plateau, Australia. *Australian Geographer* 42(1):1-17.
- Kopecky M, Cizkova S (2010) Using topographic wetness index in vegetation ecology: does the algorithm matter? *Appl. Veg. Sci.* 13:450-459.
- Link P, Simonin K, Maness H, Oshun J, Dawson T, Fung I (2014) Species differences in the seasonality of evergreen tree transpiration in a Mediterranean climate: Analysis of multiyear, half-hourly sap flow observations, *Water Resour. Res.*, 50, 1869–1894, doi:10.1002/ 2013WR014023.
- Lohammar T, Larsson S, Linder S, Falk SO (1980) FAST: Simulation models of gaseous exchange in Scots Pine, in *Structure and Function of Northern Coniferous Forests: An Ecosystem Study*, *Ecol. Bull.*, vol. 32, ed. T. Persson, pp. 505–523, Stockholm, Oikos Editorial Office.
- López-Bernal A, Alcántara E, Villalobos FJ (2014) Thermal properties of sapwood of fruit trees as affected by anatomy and water potential: errors in sap flux density measurements based on heat pulse methods. *Trees*, 28:1623–1634.



- Loranty MM, Mackay DS, Ewers BE, Adelman JD, Kruger EL (2008) Environmental drivers of spatial variation in whole-tree transpiration in an aspen-dominated upland-to-wetland forest gradient, *Water Resour. Res.*, 44, W02441, doi:10.1029/2007WR006272.
- Loustau, D., and A. Granier. 1993. Environmental control of water flux through Maritime pine (*Pinus pinaster* Ait.), in *Water transport in plants under climatic stress*, eds. M. Borghetti, J. Grace, and A. Raschi, Cambridge University Press, Cambridge, UK. pp. 205-218
- Mackay DS, Band LE (1997) Forest ecosystem processes at the watershed scale: Dynamic coupling of distributed hydrology and canopy growth, *Hydrol. Processes*, 11:1197–1217.
- Mackay DS, Ewers Be, Loranty MM, Kruger EL (2010) On the representativeness of plot size and location for scaling transpiration from trees to a stand, *J. Geophys. Res.*, 115, G02016, doi:10.1029/2009JG001092.
- Maherali H, DeLucia EH (2001) Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia* 129:481–491
- Matyssek R, Wieser G, Patzner K, Blaschke H, Häberle K-H (2009) Transpiration of forest trees and stands at different altitude: consistencies rather than contrasts? *Eur J. Forest Res.* 128:579-596.
- McDowell NG, Phillips N, Lunch CK, Bond BJ, Ryan MG (2002) An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiol.* 22:763–774.
- McNab WH (1989) Terrain shape index: Quantifying effect of minor landforms on tree height. *Forest Science*, 35: 91–104.
- McNab WH (1993) A topographic index to quantify the effect of mesoscale landform on site productivity. *Can. J. of For. Res.*, 23:1100– 1107.
- Meinzer F (2003) Functional convergence in plant responses to the environment. *Oecologia* 134:1-11.
- Montero P, Vilar JA (2014) TSclust: An R Package for Time Series Clustering. *Journal of Statistical Software*, 62(1), 1-43. <http://www.jstatsoft.org/v62/i01/>.
- Monteith JL (1995) A reinterpretation of stomatal responses to humidity. *Plant Cell Environ.* 18:357–364.

- Nimlos TJ (1986) Soils of Lubrecht Experimental Forest. Miscellaneous Publication No. 44. Missoula, MT, Montana Forest and Conservation Experiment Station: 36.
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.
- Oren R, Phillips N, Katul G, Ewers BE, Pataki DE (1998) Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. *Ann. Sci. For.* 55:191– 216.
- Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment*, 22:1515–1526.
- Pataki DE, Oren R, Smith WK (2000) Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology* 81:2557–2566.
- Phillips N, Nagchaudhuri A, Oren R, Katul G (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* 11:412–419.
- Phillips NG, Oren R, Licata J, Linder S (2004) Time series diagnosis of tree hydraulic characteristics. *Tree Physiol.* 24, 879– 890.
- Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ (2014) Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. *Ecol. Lett.* 17:82-91.
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Roddy AB, Winter K, Dawson DE (2015) Responses of petiole sap flow to light and vapor pressure deficit in the tropical tree *Tabebuia rosea* (Bignoniaceae). *PeerJ PrePrints* 3:e1252 <https://dx.doi.org/10.7287/peerj.preprints.1017v1>
- Sala A (2006) Hydraulic compensation in Northern Rocky Mountain conifers: does successional position and life history matter? *Oecologia* 149, 1–11.
- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. *Science* 148:339–346.

- Shinohara Y, Tsuruta K, Ogura A, Noto F, Komatsu H, Otsuki K, Maruyama T (2013) Azimuthal and radial variations in sap flux density and effects on stand-scale transpiration estimates in a Japanese cedar forest. *Tree Physiol.* 33:550-558.
- Soetaert K, Petzoldt T (2010) Inverse Modelling, Sensitivity and Monte Carlo Analysis in R Using Package FME. *Journal of Statistical Software*, 33(3):1-28. URL <http://www.jstatsoft.org/v33/i03/>.
- Swanson RH (1983) Numerical and experimental analyses of implanted- probe heat pulse velocity theory. PhD thesis, University of Alberta.
- Tardieu F, Davies WJ (1993) Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants, *Plant Cell Environ.* 16:341–349, doi:10. 1111/j.1365-3040.1993.tb00880.x.
- Tetens VO (1930) Uber einige meteorologische. Begriffe, *Zeitschrift fur Geophysik.* 6:297-309.
- Thompson S, Harman C, Heine P, Katul G (2010) Vegetation-infiltration relationships across climatic and soil type gradients, *J. Geophys. Res.-Biogeo.*, 115:1–27.
- Thompson SE, Harman CJ, Troch PA, Brooks PD, Sivapalan M (2011) Spatial scale dependence of ecohydrologically mediated water balance partitioning: A synthesis framework for catchment ecohydrology. *Water Resour. Res.* 47, W00J03, doi:10.1029/2010WR009998.
- Traver E, Ewers BE, Macky DS, Loranty MM (2009) Tree transpiration varies spatially in response to atmospheric but not edaphic conditions. *Funct. Ecol.* 24:273–282
- Tromp-van Meerveld HJ, McDonnell JJ (2006) On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale, *Adv. Water Resour.*, 29(2):293 – 310.
- Vandegehuchte MW, Steppe K (2012) Improving sap flux density measurements by correctly determining thermal diffusivity, differentiating between bound and unbound water. *Tree Physiol.* 32:930–942.
- Waring RH, Landsberg JJ (2011) Generalizing plant–water relations to landscapes, *J. Plant Ecol.*, 4(1-2):101–113.
- Zhu AX (2000) Mapping soil landscape as spatial continuua: The neural network approach. *Water Resour. Res.* 36(3):663-677.

CHAPTER THREE

UNCERTAINTY IN CONIFER TRANSPIRATION  
DUE TO SAPWOOD TRAITS

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Nathaniel Thomas Looker

Contributions: Conceived study design and analyses. Conducted field work and analyses. Drafted the manuscript.

Co-Author: Justin Martin

Contributions: Assisted with field work. Provided feedback on the manuscript.

Co-Author: Kelsey Jencso

Contributions: Contributed to conceptual framework of the project.

Co-Author: Jia Hu

Contributions: Contributed to conceptual framework of the project. Conceived study design and analyses. Assisted with field work. Revised the manuscript.

Manuscript Information Page

Nathaniel Thomas Looker, Justin Martin, Kelsey Jencso, Jia Hu  
Agricultural and Forest Meteorology

Status of Manuscript:

☐ Prepared for submission to a peer-reviewed journal

☒ Officially submitted to a peer-review journal

☐ Accepted by a peer-reviewed journal

☐ Published in a peer-reviewed journal

Published by Elsevier BV

Submitted April 16, 2015

## UNCERTAINTY IN CONIFER TRANSPIRATION DUE TO SAPWOOD TRAITS

### 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 stomatal uptake of carbon dioxide. Despite its hydrologic and ecological significance, transpiration remains a notoriously challenging process to measure in heterogeneous landscapes. In individual plants, sap flow sensors permit estimation of transpiration by using heat as a tracer of sap movement (variously interpreted as sap velocity or sap flux density; Edwards et al. 1997), which yields volumetric water flow when multiplied by the conductive cross-sectional area of the stem (Marshall 1958). 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.

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. Scaling 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 “scale factors.” While previous studies have quantified variability in scale factors (e.g., Hatton et al. 1992, Vergeynst et al. 2014) and related uncertainty in scale factors to error in transpiration estimates (Muñoz-Villers et al. 2012, Ford et al. 2007), systematic handling of error remains absent in much of the sap flow literature. The widespread practice of expressing uncertainty in transpiration 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 scale factors and, consequently, may overstate the precision of transpiration estimates. Focusing on the widely used heat-ratio method (HRM) design of heat-pulse sensors (Burgess et al. 2001), the present study explores how the simultaneous variation of scale factors contributes to uncertainty of tree-level transpiration. Additionally, to prioritize field measurements of scale factors, I assess variability of scale factors across the levels of a nested hillslope hydrological study design. First, I provide a brief overview of common practices in scaling HRM measurements to tree-level transpiration.

### Scaling to 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<sup>-1</sup>) is then calculated as

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

where  $x$  is heater-to-thermocouple spacing in the axial direction (cm),  $k$  is sapwood thermal diffusivity (cm<sup>2</sup> s<sup>-1</sup>), and  $v_u$  and  $v_d$  are the respective up- and downstream temperature rises (K). Following Burgess et al. (2001), researchers typically set  $k$  to a nominal value of  $2.5 \times 10^{-3}$  cm<sup>2</sup> s<sup>-1</sup> (hereafter  $k_{nom}$ ), which is intermediate between thermal diffusivities of water ( $1.4 \times 10^{-3}$  cm<sup>2</sup> s<sup>-1</sup>) and of dry wood ( $4.0 \times 10^{-3}$  cm<sup>2</sup> s<sup>-1</sup>). Burgess et al. (2001) also outline a procedure for calculating a theoretical  $k$  ( $k_{theo}$ ):

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

where  $K_{gw}$  is thermal conductivity (J m<sup>-1</sup> s<sup>-1</sup> °C<sup>-1</sup>),  $\rho_{gw}$  is density (kg m<sup>-3</sup>), and  $c_{gw}$  is specific heat capacity (J kg<sup>-1</sup> °C<sup>-1</sup>) 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<sup>-1</sup>), and basic density,  $\rho_b$  (kg m<sup>-3</sup>). 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  $\rho_b$  is the ratio of  $w_d$  to sample volume,  $vol$  (m<sup>3</sup>).

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  $k_{theo}$ . As  $V_h$  is directly proportional to  $k$  (Eqn. 1), differences between  $k_{theo}$  and  $k_{nom}$  induces the same magnitude of error in  $V_h$ . However, 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  $V_s$  ( $\text{cm h}^{-1}$ ) 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  $\rho_s$  is the density of sap; the three latter terms are treated as constants (Burgess et al. 2001). Hence,  $m_c$  and  $\rho_b$  influence HRM transpiration estimates first through the calculation of  $k_{theo}$  (Eqn. 2) and subsequently through the conversion of  $V_h$  to  $V_s$  (Eqn. 3), so that the sensitivity of  $V_s$  to error in  $m_c$  and  $\rho_b$  depends on the net behavior of these variables in both scaling steps (Fig. 3.1).

With the assumption of constant trunk water storage, transpiration is equal to stem volumetric water flow,  $Q$  (volume water per tree per unit time), which is the product of  $V_s$  and conductive sapwood area,  $A_s$  ( $\text{cm}^2$ ):

$$Q = V_s A_s. \quad (\text{Eqn. 4})$$

$A_s$  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. Because  $V_s$  varies radially (i.e., along the bark-to-pith axis) and azimuthally (i.e., around the stem circumference), transference of flow rates from one to three dimensions requires assumptions about the distribution of  $V_s$  across  $A_s$ . Generally, radial variability in  $V_s$  is characterized by measuring  $v_u$  and  $v_d$  at multiple depths and integrating according to a linear or curvilinear function (Alvarado-Barrientos et al. 2013).

Researchers concerned with azimuthal variability may install probes in multiple sides of a tree (Köstner et al. 1998). 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).

### 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 these scale factors (triangles in Fig. 3.1). Yet because sensor design and datalogger limitations result in sampling tradeoffs, consideration of variability in all the aforementioned scale 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). In studies with the objective of estimating total volume of water transpired at the stand or catchment scale (e.g., many hydrological applications of sap flow), 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, I sought to quantify the uncertainty in tree-level transpiration due to variability in sapwood properties, including  $R_s$ , while also focusing on  $m_c$  and  $\rho_b$  in light of the widespread use of  $k_{nom}$  rather than  $k_{theo}$ . I address two specific objectives through empirical and theoretical means:

- 1) Determine how variability in  $m_c$  and  $\rho_b$  contributes to error in whole-tree water use ( $Q$ ) in the midst of simultaneous variation in other scale factors
- 2) Characterize variability of  $m_c$ ,  $\rho_b$ , and  $R_s$  across a range of spatial scales, from the level of individual trees to site and species levels.

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

## Materials and Methods

### Study Site

I conducted my 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 I established in summer 2013 in the 18-km<sup>2</sup> watershed of the North Fork of Elk Creek. At low (1400 m) and high (1800 m) elevations, I selected one north-facing and one south-facing convergent hillslope for my study; this resulted in a total of four hillslopes across the watershed (Fig. 2.1). 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. To more thoroughly characterize the intraspecific variability of scale factors (Objective 2), I also measured  $m_c$ ,  $\rho_b$ , and  $R_s$  in Douglas-fir in two additional 1800-m sites near Bozeman, Montana (henceforth BZN), 225 km southwest of LEF. The BZN sites were on relatively planar slopes, with one north- and one south-facing site. LEF and BZN sites were each subdivided into two 20 m-diameter plots.

## Field Measurements

Sap Flow. To quantify realistic variability in  $V_h$  for use in my simulation of the scaling procedure (Objective 1), I estimated  $V_h$  using HRM sensors (Burgess et al. 2001) that I constructed according to Hu et al. (2010). In this implementation of the HRM, a 3.7-cm nichrome line heater (18-20  $\Omega$ ) 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 two depths: 2 cm ( $R_{outer}$ ) and 3.7 cm ( $R_{inner}$ ) 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  $x = 0.6 \text{ cm}$ .

I 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, I installed HRM sensors in four dominant individuals of Douglas-fir and four of either ponderosa pine, subalpine fir, Engelmann spruce, or western larch, depending on which species were present (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. I selected trees to prioritize crown symmetry and site-level representativeness of DBH. The following analyses were conducted on two one-week periods of  $V_h$  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. I accounted for misalignment by assuming zero flow during the night (0:00 to 5:00 h) and during conditions of low vapor pressure deficit ( $<1.0$  kPa). I then subtracted mean  $V_h$  recorded under these conditions from the time course of  $V_h$  for each pair of thermocouples. The uncertainty associated with the misalignment correction has been addressed elsewhere (e.g., Bleby et al. 2004, Gotsch et al. 2014); the present study omitted this source of error due to lack of “true zero” data, obtained by severing the sapwood and recording apparent flow.

Scale Factors. Of the measurements required to estimate  $Q$  from observations of  $v_d/v_u$  (Fig. 3.1), I focused on  $m_c$  and  $\rho_b$  in order to characterize the sensitivity of  $Q$  to uncertainty in these variables (Objective 1) and also to address how  $m_c$  and  $\rho_b$  as well as  $R_s$  vary within and across species (Objective 2). To estimate  $m_c$  and  $\rho_b$  from  $w_f$ ,  $w_d$ , and  $vol$ , I 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 ( $n=33$ ,  $n=48$ , respectively) and from Douglas-fir individuals in the BZN sites in October and November 2014 ( $n=16$ ). At LEF, I 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. I 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. In each of the four BZN stands, I 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. I 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  $\rho_b$ . 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  $w_d$ . I used  $w_f$ ,  $w_d$ , and  $vol$  to calculate  $m_c$  and  $\rho_b$  and then obtained  $k_{theo}$  following Burgess et al. (2001;  $k_{Burg}$ ) and the alternative method of Vandegehuchte and Steppe et al. (2012;  $k_{Vand}$ ). The two methods both use Eqn. 2 but differ in that the calculation of  $k_{Vand}$  accounts for the distinct effects of free water and water bound to the wood matrix on sapwood thermal conductivity,  $K_{gw}$ . The use of  $k_{Burg}$  rather than  $k_{Vand}$  may impart error in  $V_s$  exceeding 10% (López-Bernal et al. 2014).

I measured  $R_s$  and bark thickness ( $bark$ , cm) on the east and west side 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:

$$A_s = \pi(\text{DBH}/2 - bark)^2 - \pi(\text{DBH}/2 - bark - R_s)^2. \quad (\text{Eqn. 5})$$

## Analyses

Objective 1. In addressing Objective 1, I was primarily concerned with the net effect of variability in  $m_c$  and  $\rho_b$  on the uncertainty of the scaling output  $Q$ . Towards this end, I simulated 10,000 observations (i.e., representing hypothetical trees) of  $V_h$  and scale factors (listed and defined in Table 3.1) and then scaled  $V_h$  to  $Q$  for each combination of simulated scale factors. In order to constrain the simulation to combinations of scale factor values that realistically represented each species, I used actual sap flow data and scale factor measurements from LEF. First, I derived two variables to represent within-tree variability in  $V_h$  (*Azim* and *Rad*) and one variable to represent maximum possible  $V_h$  for each tree ( $V_{h\_max}$ ). To characterize azimuthal variability in  $V_h$  (i.e., the distribution of  $V_h$  around the trunk circumference), I defined the variable *Azim* as the proportion of  $V_h$  at a radial depth of 2.0 cm on the east side of a tree to  $V_h$  at the same depth on the west side of the tree. Similarly, for both east- and west-side probes, I characterized the radial distribution of  $V_h$  by defining the variable *Rad* as the proportion of  $V_h$  at a radial depth of 3.7 cm to that at 2.0 cm. Both *Azim* and *Rad* were calculated using mean  $V_h$  between 9:00 and 18:00 h. To describe intra- and interspecific variation in maximum  $V_h$ , I constructed a mean diurnal curve of  $V_h$  for each individual tree by averaging observations at the same hour across the days of the study period (Fig. 3.2); from these diurnal curves, I extracted the maximum value of  $V_h$  ( $V_{h\_max}$ ) for each tree.

Due to correlations between specific pairs of scale factors, I fit the following simple linear regressions (SLRs) for each species using my measurements from LEF:  $R_s$  and *bark* as functions of DBH;  $w_f$  as a function of  $\rho_b$ ; and *Rad* as a function of  $R_s$  (Table

3.2). Additionally, to represent within-tree variability in  $R_s$  and *bark*, I calculated the coefficient of variation (CV), defined as the sample standard deviation divided by the sample mean, for observations of both variables in each individual tree.

I employed a combination of parametric and nonparametric sampling schemes to generate values for each variable (Table 3.1) in R version 3.1.1 (R Core Team 2014). I initiated each set of inputs by randomly sampling a DBH and selecting one of the five species studied. Next, the species-specific SLRs were used to predict  $R_s$  and *bark* as functions of DBH on an arbitrary side 1 of the trunk; the variable representing the radial distribution of  $V_h$  (*Rad*) was then predicted based on  $R_s$ . Each simulated tree was assigned a hypothetical sapwood sample of a fixed volume and a random dry weight  $w_d$  (a function of volume and basic density  $\rho_b$ ). Because a negative relationship between  $m_c$  and  $\rho_b$  was observed across species (Fig. 3.3), a random  $m_c$  was constrained by an SLR with  $\rho_b$  as the predictor. An error term was added to the SLR-predicted variables by sampling from a normal distribution fit to the residuals of each regression. To incorporate the observed within-tree variability in  $R_s$  and *bark*, each input set sampled a CV for  $R_s$  and for *bark* from vectors of the CVs obtained from the LEF data. Given the definition of the CV (standard deviation divided by the mean),  $R_s$  and *bark* were generated for side 2 of each simulated tree by sampling from a normal distribution with a mean of the  $R_s$  or *bark* value on side 1 and a standard deviation equal to the product of the sampled CV and the  $R_s$  or *bark* value on side 1. The radial positions of the inner and outer thermocouples ( $R_{inner}$  and  $R_{outer}$ ) were set to 3.7 and 2.0 cm, except when sapwood depth ( $R_s$ ) was less than the default probe length (3.7 cm), in which case  $R_{inner}$  and  $R_{outer}$  were respectively set



to 75 and 50% of  $R_s$ . Finally, each tree received a maximum possible  $V_h$  ( $V_{h\_max}$ ) sampled from the values observed in each species.

After establishing the scale factors for 10,000 model trees,  $V_{h\_max}$  was scaled to  $Q$  using  $k\_nom$ ,  $k\_Vand$ , and  $k\_Burg$  for each tree. I first defined the randomly sampled  $V_{h\_max}$  as  $V_h$  at a radial depth of 2.0 cm (or 50% of  $R_s$ ) on an arbitrary side 1 of the trunk; I then generated values for  $V_h$  at 3.7 cm (or 75% of  $R_s$ ) on the same side of the trunk (using  $Rad1$ ). In the same manner, I modeled  $V_h$  at depths of 2.0 cm (or 50% of  $R_s$ ) and 3.7 cm (or 75% of  $R_s$ ) on side 2 of the trunk using  $Azim$  and  $Rad2$ . For each tree,  $m_c$ ,  $\rho_b$ , and  $k\_theo$  in the measured domain were calculated using  $w_f$ ,  $w_d$ , and  $vol$  of the simulated sapwood sample. For each thermocouple position,  $V_{h\_k\_nom}$  was converted to  $V_{h\_k\_theo}$  by replacing  $k\_nom$  with  $k\_theo$  (i.e.,  $V_{h\_k\_theo} = V_{h\_k\_nom} (k\_theo / k\_nom)$ , where  $k\_theo$  is either  $k\_Burg$  or  $k\_Vand$ ). The subsequent scaling steps were conducted on both  $V_{h\_k\_nom}$  and  $V_{h\_k\_theo}$  in order to evaluate the relative error in  $Q$  incurred by using  $k\_nom$  rather than  $k\_theo$ .

Wounding in the sapwood is typical after probe insertion, resulting in underestimation of  $V_h$  that can be corrected using a polynomial function and coefficients that depend on wound size (Burgess et al. 2001). I simulated the contribution of the wounding correction to uncertainty in  $Q$  by assigning each input set a wound size ( $wound$ ) and applying the polynomial correction of Burgess et al. (2001), yielding  $V_c$ , which is then used in place of  $V_h$  in the calculation of  $V_s$  (Eq. 3).

Next, to express sap flow volumetrically, I divided the measured domain into two concentric rings, such that the thermocouple positions ( $R_{inner}$  and  $R_{outer}$ ) 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). When  $R_s$  exceeded the length of the probe, I 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. Because the azimuthal distribution of  $V_s$  and  $R_s$  between the two probes was unknown in our implementation of the HRM, I weighted volumetric flow on the two sides of the tree with a randomly assigned proportion, *Circ* (Table 3.1). For example, if both halves of the tree contributed equally to total  $Q$ , then I would set *Circ* to be 0.5; however, if sapwood depth or leaf area were distributed asymmetrically around the trunk circumference, then *Circ* would be set accordingly. Finally,  $Q$  on sides 1 and 2 of the trunk was weighted by *Circ* and summed to obtain whole tree  $Q$ .

To quantify the potential error associated with using  $k_{nom}$  rather than  $k_{theo}$  in the calculation of  $V_h$  (Step II in Fig. 3.1), I assessed the distribution of the scaling coefficient  $k_{theo}/k_{nom}$  (i.e., theoretical thermal diffusivity as a proportion of the nominal value) by plotting isolines of  $k_{theo}/k_{nom}$  in  $m_c$ - $\rho_b$  trait space (Fig. 3.3A). These isolines indicate the values of  $m_c$  that would yield  $k_{theo}$  equal to 25, 50, 75, or 100% of  $k_{nom}$  across a range of  $\rho_b$ . The error resulting from use of  $k_{nom}$  rather than  $k_{theo}$  was quantified as the relative error in  $Q$  ( $Q_{RelErr}$ )

$$Q_{RelErr} = (Q_{k_{nom}} - Q_{k_{theo}}) / Q_{k_{theo}}. \quad (\text{Eqn. 6})$$

I evaluated the robustness of my results to the method of determining  $k_{theo}$  by calculating  $Q_{RelErr}$  for  $k_{Burg}$  and  $k_{Vand}$  separately.

I explored the second effect of  $m_c$  and  $\rho_b$  on  $Q$  (through the conversion of  $V_h$  to  $V_s$ , Step IV in Fig. 3.1) by rearranging Eq. 3 to obtain the scaling coefficient  $V_s/V_h$  and then plotting isolines of this value in  $m_c$ - $\rho_b$  trait space (Fig. 3.3B). 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, I may expect  $V_s/V_h > 1$ . Because the two scaling coefficients ( $k_{theo}/k_{nom}$  and  $V_s/V_h$ ) have multiplicative effects within the procedure of scaling from recorded  $V_h$  (with  $k_{nom}$ ) to  $V_s$ , I defined the net effect  $N$  (%) of the scaling steps dependent on  $m_c$  and  $\rho_b$  as:

$$N = 100 (V_s/V_h) (k_{theo}/k_{nom}) \quad (\text{Eqn. 7}).$$

Hence,  $N$  is equivalent to the percentage by which  $V_h$  (as recorded in the field) changes within the scaling procedure due to  $m_c$  and  $\rho_b$ ; for example, when  $N$  is 50%, estimated  $V_s$  will be half the value of recorded  $V_h$ , while  $N$  of 100% indicates that  $V_h$  and  $V_s$  are equal. The individual contributions of  $m_c$  and  $\rho_b$  to  $N$  were quantified with semi-partial correlation coefficients ( $r$ ).

Objective 2. My second objective was to identify the levels of the sampling hierarchy that explained the most variability in  $m_c$ ,  $\rho_b$ , and  $R_s$ . Following the approach of Messier et al. (2010), I fit linear mixed-effects models in R (lme4 package) to partition variance in  $m_c$ ,  $\rho_b$ , and  $R_s$  across sampling levels (site, plot, species, and tree). I treated each level as a random effect and expressed the variance in the response at each level as a percentage of the sum of variance across levels. In the multispecies models fit to LEF data, I treated site ( $n=4$ ), plot ( $n=2$  per site), species ( $n=5$ ), and tree ( $n=3-6$  per plot) as random effects. I limited the analysis of  $m_c$  and  $\rho_b$  to the core samples representing the

outermost 2 cm of xylem because of the dramatic contrast in these traits between sapwood and heartwood. After pooling the data for Douglas-fir from LEF and BZN, I fit models of  $m_c$ ,  $\rho_b$ , and  $R_s$  in which the random effects included location (LEF or BZN), site (n=4 at LEF and n=2 at BZN), plot (n=2 per site), and tree (n=3-6 per plot). To account for the linear relationship between DBH and  $R_s$ , DBH was included as a fixed effect in the models of  $R_s$ .

## Results

### Field Measurements

In order to characterize intra- and interspecific variability in sap flow rates and the scale factors necessary to estimate  $Q$ , I measured  $V_h$  and wood properties in five coniferous species. Cross-species distinctions were evident in the  $V_h$ -derived variables as well as in  $m_c$ ,  $\rho_b$ , and  $R_s$  (Table 3.3). The maximum observed  $V_h$  extracted from mean diurnal curves ranged from 6.3 cm h<sup>-1</sup> in subalpine fir to 27.8 cm h<sup>-1</sup> in Douglas-fir, with non-averaged instantaneous rates as high as 61.5 cm h<sup>-1</sup> in western larch. The proportion of  $V_h$  at 3.7 cm to 2.0 cm ( $Rad$ ) ranged from 0.24 (SE=0.020) in subalpine fir to 1.02 (0.15) in Engelmann spruce, likely reflecting variability in both the radial distribution of  $V_h$  and the fraction of sapwood measured (due to fixed probe length but variable  $R_s$ ). Azimuthal symmetry expressed as  $Azim$  ranged from 1.13 (SE=0.16) in Douglas-fir to 1.54 (0.059) in western larch; that is, rates of  $V_h$  measured on one side of a tree could be as much as 54% higher than those on the opposite side of the same tree. Mean  $\rho_b$  was 389 (SE=20), 390 (14), 442 (9.9), 472 (7.7), and 559 (27) kg m<sup>-3</sup> in Engelmann spruce,

subalpine fir, ponderosa pine, Douglas-fir, and western larch, respectively. The greatest within-tree variability in  $\rho_b$  was observed in western larch (mean tree CV = 0.13). Water content,  $m_c$ , declined with increasing  $\rho_b$  both within species (Fig. 3.3) and among species (see regressions in Table 3.3), with species-level mean  $m_c$  ranging from 1.3 (SE=0.14) kg kg<sup>-1</sup> in western larch to 2.3 (0.23) kg kg<sup>-1</sup> in Engelmann spruce. Within-tree variability in  $m_c$  was as high as 0.29 (CV) in subalpine fir.

In light of recent debate on the calculation of sapwood thermal diffusivity,  $k$  (López-Bernal et al. 2014, Vandgehuchte and Steppe 2012), I conducted our analyses using a fixed value of  $k$  and two approaches to estimate a theoretical  $k$  ( $k_{theo}$ ). First, I set  $k$  to the nominal value ( $k_{nom}$ ,  $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ ) proposed by Marshall (1958) and justified by Burgess et al. (2001). I then used the approach of Burgess et al (2001) to estimate  $k$  ( $k_{Burg}$ ) based on sapwood  $m_c$  and  $\rho_b$ . Finally, I employed the method of Vandgehuchte and Steppe (2012) that differentiates between free water and water bound to the wood matrix ( $k_{Vand}$ ). Calculated  $k_{Burg}$  was less than  $k_{nom}$  for all combinations of  $m_c$  and  $\rho_b$  observed in the LEF or BZN cores, with a maximum of  $1.9 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$  and a mean of  $1.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$  (Fig. 3.4). While these values of  $k$  are lower than those typically obtained in sap flow studies (e.g., Goldsmith et al. 2013), the range of  $k_{Burg}$  calculated for my sapwood cores was in agreement with estimates from wood science (Maku 1954, Steinhagen 1977, Simpson and TenWolde 1999) and micrometeorology literature (Herrington 1969). The method of Vandgehuchte and Steppe (2012) yielded systematically higher values of  $k_{theo}$ : maximum  $k_{Vand}$  was  $2.6 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ , with a mean of  $2.1 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ .

After  $m_c$  and  $\rho_b$ , the third scale factor of primary interest was sapwood depth,  $R_s$ , which typically serves as the basis for estimating sapwood area,  $A_s$ . Measurements of  $R_s$  revealed a positive relationship with DBH across species (Table 3.2), with different intercepts for the relationship in Engelmann spruce and ponderosa pine compared to that in subalpine fir, western larch, and Douglas-fir. Within-tree variability in  $R_s$  may explain the observed azimuthal variability ( $Azim$ ) of  $V_h$ : in Douglas-fir, a regression of  $Azim$  on the ratio of east- to west-side  $R_s$  had a slope of 1 ( $p = 0.034$ ). Western larch exhibited the greatest within-tree variability in  $R_s$  (mean tree CV = 0.24), while ponderosa pine showed the least (CV = 0.046).

### Analyses

Objective 1. The variability incorporated into the simulation of inputs permitted exploration of the behavior of the scaling procedure when executed using combinations of  $V_h$  and scale factors beyond those directly observed in my study; consequently, my results indicate the conditions under which the outcomes of the scaling procedure follow theoretical expectations (Marshall 1958, Burgess et al. 2001). Input sets for which  $k_{theo}/k_{nom} > 1$  (8.6% and 2.1% of cases when using  $k_{Vand}$  and  $k_{Burg}$ , respectively) featured much lower  $m_c$  (mean =  $0.567 \text{ kg kg}^{-1}$ , SE = 0.0084) than observed in the core samples (mean =  $1.68 \text{ kg kg}^{-1}$ , SE = 0.47). The value of  $k_{theo}/k_{nom}$  also depended on  $\rho_b$ , so that  $k_{theo}/k_{nom}$  calculated at a particular combination of  $\rho_b$  and  $m_c$  could also be obtained if  $\rho_b$  decreased and  $m_c$  increased (Fig. 3.3A). The decline in  $k_{theo}$  with increasing  $m_c$  resulted in a species-specific relationship between  $m_c$  and  $Q_{RelErr}$  (Fig.

3.5), with greater sensitivity and possible error when  $k_{theo}$  is calculated according to Burgess et al. (2001).

The distribution of  $V_s/V_h$  in  $m_c$ - $\rho_b$  space was similar to that of  $k_{theo}/k_{nom}$ : a decrease in  $\rho_b$  and increase in  $m_c$  could result in no change in  $V_s/V_h$  (Fig. 3.3B). However, because  $V_s/V_h$  increases with  $\rho_b$  and  $m_c$  in Eqn. 3, the two scaling coefficients varied inversely (Fig. 3.6). 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. 3.7) despite the negative influence of  $m_c$  on  $k_{theo}/k_{nom}$ . The semi-partial correlation between  $N$  and  $m_c$  ( $r = 0.981$  for the Burgess et al. method,  $r = 0.939$  for the Vandegehuchte and Steppe method) was greater than that between  $N$  and  $\rho_b$  ( $r = 0.665$  for the Burgess et al. method,  $r = 0.726$  for the Vandegehuchte and Steppe method).

The variables  $k_{theo}$  and  $V_s/V_h$  as calculated with observed  $m_c$  and  $\rho_b$  both deviated from expectations. For the majority of sapwood samples,  $k_{theo}$  was about 50% of  $k_{nom}$ , with the greatest values observed in western larch at a radial depth of 2-4 cm (representing heartwood in most individuals). Mean  $k_{theo}$  was comparable to  $k$  of water ( $1.4 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ ) when using the approach of Burgess et al. (2001); the method of Vandegehuchte and Steppe (2012) produced higher values, but mean  $k_{theo}$  remained 15% less than  $k_{nom}$ .

Objective 2. In partitioning variance in  $m_c$ ,  $\rho_b$ , and  $R_s$ , I found that the level of the sampling hierarchy contributing the most variability depended on the trait in question. Species explained 57% of the variability in  $R_s$  after accounting for DBH, while only 23%

of the variability in  $\rho_b$  and 6.5% of the variability in  $m_c$  was associated with species (Fig. 3.8A). Though site also contributed to variability in  $m_c$  and  $\rho_b$ , the majority of variance in these traits remained unexplained (88% and 73% of total variance, respectively). The models for Douglas-fir illuminated the relative contributions of sampling levels to variability of traits within a species: 63% of the residual variance in  $R_s$  after accounting for DBH occurred at the among-tree level, while location (LEF or BZN) accounted for 51% of the variance in  $m_c$ . The among-tree level contributed to 25% of the variability in  $\rho_b$  in Douglas-fir, leaving nearly half the variability in that trait unexplained.

### Discussion

Sap flow sensors are widely used in hydrological and ecological studies to estimate whole-tree transpiration  $Q$  on the basis of the movement of heat through the sap stream. Inference on  $Q$  is only possible after the proxy measurement (e.g., temperature rise in the sap stream, in the case of the heat-ratio method) is scaled up, which involves numerous avenues for the introduction and propagation of error. Variability in the physiological and structural data required for scaling up and their relative effects on the outcome of the scaling procedure 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. 2014, Gotsch et al. 2014), though not necessarily in tandem. Published sap flow error analyses have generally followed a one-at-a-time approach, assessing each source of error individually and hence ignoring interactive 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), I developed an approach to characterize uncertainty in  $Q$  attributable to  $m_c$  and wood density,  $\rho_b$ , while also acknowledging additional sources of error. I also pursued the complementary objective of identifying the levels of a sampling hierarchy that contribute most substantially to overall variability in  $m_c$ ,  $\rho_b$ , and sapwood depth,  $R_s$ . Taken together, my findings can help prioritize efforts to sample scale factors and improve confidence in estimates of  $Q$ .

#### 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 ( $K_{gw}$ ,  $\rho_{gw}$ , and  $c_{gw}$ ), which are sensitive to variation in  $m_c$  and  $\rho_b$  (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 transpiration estimates. However,  $m_c$  and  $\rho_b$  do not vary in isolation, and other scale factors (such as  $A_s$ ) also impart uncertainty to the process of scaling recorded measurements of  $V_h$  to tree-level  $Q$ . In evaluating the sensitivity of the scaling procedure to  $m_c$  and  $\rho_b$  given simultaneous variability in other scale factors, I found that  $V_s$  ranged from 29 to 120% of  $V_h$  calculated with  $k_{nom}$ . This percentage ( $N$ ) represents the effect of substituting  $k_{theo}$  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  $k_{theo}$  based on  $m_c$  and  $\rho_b$ , 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  $k_{theo}$  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. My simulation indicated that  $k_{theo}$  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. 3.5). Though  $k_{theo}$  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  $k_{theo}$  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).

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  $\rho_b$  for which  $V_s/V_h$  was greater than 1 were associated with declines in  $k_{theo}$  (Fig. 3.6); hence,  $m_c$  exerts *opposing* effects on the scaling process through the two steps (II and IV in Fig. 3.1), with a net positive effect (Fig. 3.7) on the process of scaling from  $V_h$  (with  $k_{nom}$ ) to  $Q$ . The scaling process is also influenced by  $\rho_b$ , both through its relationship with  $m_c$  and independently, though the effect of  $\rho_b$  on percentage change  $N$  is less apparent than the linear relationship between  $m_c$  and  $N$  (Fig. 3.7).

The Scale Factors  $m_c$ ,  $\rho_b$ , and  $R_s$   
 Exhibit Contrasting Patterns of Variability  
Within and Among Trees, Species, and Sites.

Gravimetrically estimated  $m_c$  and  $\rho_b$  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), and the within-tree radial variation in  $m_c$  and  $\rho_b$  (data not shown) is consistent with physiological theory (Stewart 1967). However, I observed an unexpected degree of variability in both  $m_c$  and  $\rho_b$  among trees within a species, with coefficients of variation as high as 0.30 ( $m_c$  in western larch) and 0.16 ( $\rho_b$  in Engelmann spruce). Using my data from Douglas-fir trees to further explore how  $m_c$  and  $\rho_b$  vary within a species, I found that variability among trees within a plot was the single largest source of uncertainty in both traits (Fig. 3.8B), apart from the variability in  $m_c$  at the broadest scale of my sampling scheme (between BZN and LEF). Similarly, after accounting for species and DBH, the largest fraction of uncertainty in  $R_s$  was observed among trees growing in the same site (Fig. 3.8A and B).

These findings indicate the importance of measuring  $m_c$ ,  $\rho_b$ , and  $R_s$  directly in the same trees in which sap flow sensors will be installed. Measurement of these traits in individuals co-occurring with instrumented trees is a common practice in sap flow studies. If logistical considerations necessitate such a substitution or the use of an allometric equation to predict sapwood area as a function of DBH, the associated uncertainty should be retained throughout the scaling procedure (e.g., with resampling, as in Magnussen and Burgess 1997). Though beyond the scope of this study, error propagation of this kind would be a simple extension of my simulated scaling procedure.

### Reducing Error in Estimates of Whole-tree Transpiration, $Q$

The final estimate of  $Q$  is sensitive to 1) the approach by which sapwood thermal diffusivity is estimated (use of a published value or estimation with the methods of Burgess et al. 2001 or Vandegehuchte and Steppe 2012) and 2) variability in the data that are the basis for that estimation ( $m_c$  and  $\rho_b$ ). Though Vandegehuchte and Steppe (2012) have emphasized how failing to differentiate between the effects of bound and free water on thermal diffusivity can incur errors in transpiration estimates, few practitioners of sap flow explicitly state which approach they used or publish the resultant value. My results suggest that spatial variability in scale factors may contribute to systematic deviation from literature-based expectations. However, because the change in  $m_c$  across individuals was associated with a corresponding change in  $\rho_b$  (Fig. 3.4),  $k_{theo}$  and  $V_s/V_h$  varied less within a species than either of the variables with which they are calculated. Hence, the variation in  $m_c$  and  $\rho_b$  at the spatial scale of this study may incur less error in  $Q$  than the variation of  $m_c$  through time (López-Bernal et al. 2014), though the relative magnitude of temporal and spatial variation in  $m_c$  remains the subject of debate (Beedlow et al. 2007).

Confidence in HRM measurements would be greatly improved with independent validation of the theoretical approaches to calculating sapwood thermal diffusivity (Burgess et al. 2001, Vandegehuchte and Steppe 2012) across a wider range of  $m_c$  and  $\rho_b$  than previous studies have considered. This validation would be particularly valuable to studies using sap flow sensors with the objective of estimating transpiration in absolute terms (i.e., total volume transpired) and in cases where the functional traits of the study

species are highly plastic or markedly different from those previously involved in method validations. Recording raw temperature data following the release of the heat pulse offers another promising means of estimating thermal diffusivity (Marshall 1958) and is increasingly feasible as data storage capacity improves.

## Tables

| Parameter or variable | Description                                                                     | Method of simulation                                                                                    |
|-----------------------|---------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------|
| <i>DBH</i>            | Trunk diameter at breast height (cm)                                            | Random sample from $U[20,50]$                                                                           |
| <i>Species</i>        | Species name                                                                    | Random sample from [Douglas-fir, subalpine fir, ponderosa pine, Engelmann spruce, western larch]        |
| $R_{sCV}$             | Within-tree coefficient of variation for sapwood depth                          | Random sample from vector of observed $R_{sCV}$                                                         |
| $R_{s1}$              | Sapwood depth (cm) on trunk side 1                                              | Species-specific regression on <i>DBH</i> + species-specific residual error                             |
| $R_{s2}$              | Sapwood depth (cm) on trunk side 2                                              | Random sample from $N(R_{s1}, R_{s1} \times R_{sCV})$                                                   |
| $R_{outer1}$          | Outer thermocouple position (cm) on trunk side 1                                | 2 if $R_{s1} > 2$ , otherwise $R_{s1} \times 0.5$                                                       |
| $R_{inner1}$          | Inner thermocouple position (cm) on trunk side 1                                | 3.7 if $R_{s1} > 3.7$ , otherwise $R_{s1} \times 0.75$                                                  |
| $R_{outer2}$          | Outer thermocouple position (cm) on trunk side 2                                | 2 if $R_{s2} > 2$ , otherwise $R_{s2} \times 0.5$                                                       |
| $R_{inner2}$          | Inner thermocouple position (cm) on trunk side 2                                | 3.7 if $R_{s2} > 3.7$ , otherwise $R_{s2} \times 0.75$                                                  |
| $bark_{CV}$           | Within-tree coefficient of variation for bark thickness                         | Random sample from vector of observed $bark_{CV}$                                                       |
| $bark_1$              | Bark thickness (cm) on trunk side 1                                             | Species-specific regression on <i>DBH</i> + species-specific residual error                             |
| $bark_2$              | Bark thickness (cm) on trunk side 2                                             | Random sample from $N(bark_1, bark_1 \times bark_{CV})$                                                 |
| $V_{h\_max}$          | Heat-pulse velocity at $R_{out1}$ ( $cm\ s^{-1}$ , nominal thermal diffusivity) | Random sample from vector of mean diurnal maximum $V_h$ (see "Sap flow" section)                        |
| $Rad_1$               | Ratio of $V_h$ at $R_{inner1}$ to $V_h$ at $R_{outer1}$                         | Species-specific regression on $R_{s1}$ + species-specific residual error                               |
| $Rad_2$               | Ratio of $V_h$ at $R_{inner2}$ to $V_h$ at $R_{outer2}$                         | Species-specific regression on $R_{s2}$ + species-specific residual error                               |
| <i>Azim</i>           | Ratio of $V_h$ at $R_{outer1}$ to $V_h$ at $R_{outer2}$                         | Random sample from normal distribution with observed species mean and standard deviation of <i>Azim</i> |
| <i>len</i>            | Length of sapwood sample (cm)                                                   | 2                                                                                                       |
| <i>diam</i>           | Diameter of sapwood sample (cm)                                                 | 0.5                                                                                                     |
| <i>vol</i>            | Volume of sapwood sample ( $m^3$ )                                              | $len \times (diam/2)^2 \times \pi \times 10^{-6}$                                                       |
| $w_d$                 | Dry weight of sapwood sample (g)                                                | Species-specific regression on <i>vol</i> + species-specific residual error                             |
| $\rho_b$              | Basic density of sapwood sample ( $kg\ m^{-3}$ )                                | $w_d / (1000 \times vol)$                                                                               |
| $w_t$                 | Wet weight of sapwood sample (g)                                                | Function of $\rho_b$ + residual error                                                                   |
| <i>wound</i>          | Width of xylem wound (cm)                                                       | Random sample from correction table in Burgess et al. (2001)                                            |
| <i>Circ</i>           | Circumferential weighting (fraction of total flow measured on trunk side 1)     | Random sample $U[0.05,0.95]$                                                                            |

Table 3.1. Parameters and variables used in the Monte Carlo simulation of the sap flow scaling procedure.  $U[x,y]$  denotes a uniform distribution ranging from  $x$  to  $y$ , and  $N(m,s)$  represents a normal distribution with mean  $m$  and standard deviation  $s$ .

| Response | Predictor | Species          | Coefficient | Intercept  | R <sup>2</sup> |
|----------|-----------|------------------|-------------|------------|----------------|
| $R_s$    | $DBH$     | Douglas-fir      | 0.04079*    | 1.42745*   | 0.1515         |
|          |           | Subalpine fir    | 0.03655*    | 1.02373*   | 0.2063         |
|          |           | Engelmann spruce | 0.07029     | 4.24274    | 0.05927        |
|          |           | Ponderosa pine   | 0.13555*    | 4.95042*   | 0.5039         |
|          |           | Western larch    | 0.03579 *   | 0.60808    | 0.1898         |
| $bark$   | $DBH$     | Douglas-fir      | 0.03213*    | 0.59776    | 0.2034         |
|          |           | Subalpine fir    | 0.05984*    | -0.84058   | 0.6922         |
|          |           | Engelmann spruce | 0.01302     | 0.27002    | 0.3195         |
|          |           | Ponderosa pine   | 0.01336     | 1.47393    | 0.0595         |
|          |           | Western larch    | 0.04789     | 0.33407    | 0.2823         |
| $Rad$    | $R_s$     | Douglas-fir      | 0.03544*    | -0.36024   | 0.3616         |
|          |           | Subalpine fir    | -           | -          | -              |
|          |           | Engelmann spruce | 0.001276    | 0.915270*  | 0.03581        |
|          |           | Ponderosa pine   | 0.002985    | 0.678990   | 0.03664        |
|          |           | Western larch    | 0.03379*    | -0.36321   | 0.4335         |
| $w_d$    | $vol$     | Douglas-fir      | 2.714e+05*  | 7.946e-02* | 0.2377         |
|          |           | Subalpine fir    | 2.382e+05*  | 5.621e-02  | 0.3124         |
|          |           | Engelmann spruce | 5.702e+05*  | -6.828e-02 | 0.5341         |
|          |           | Ponderosa pine   | 2.430e+05*  | 7.389e-02  | 0.18           |
|          |           | Western larch    | 4.764e+05*  | 3.468e-02  | 0.2213         |

Table 3.2. Estimates of coefficients and intercepts for species-specific simple linear regressions (asterisks denote estimates for which  $p < 0.05$  from a  $t$ -test).  $R_s$  = sapwood depth (cm),  $DBH$  = diameter at breast height (cm),  $bark$  = bark thickness (cm),  $Rad$  = proportion of  $V_h$  recorded at a depth of 2 cm to  $V_h$  at a depth of 3.7 cm,  $w_d$  = dry weight of sapwood sample (kg),  $vol$  = volume of sapwood sample (m<sup>3</sup>).

| Species          | DBH    | $m_c$ (0-2 cm) | $m_c$ (2-4 cm) | $\rho_b$ (0-2 cm) | $\rho_b$ (2-4 cm) | $R_s$       | bark        | $V_{h\_max}$ | Azim        | Rad         |
|------------------|--------|----------------|----------------|-------------------|-------------------|-------------|-------------|--------------|-------------|-------------|
| Douglas-fir      | 38 (1) | 1.81 (0.06)    | 1.40 (0.09)    | 473 (8)           | 477 (9)           | 2.93 (0.12) | 1.79 (0.09) | 27.8 (3.1)   | 1.19 (0.06) | 0.38 (0.22) |
| Subalpine fir    | 32 (2) | 1.92 (0.16)    | 1.24 (0.05)    | 408 (16)          | 372 (14)          | 2.15 (0.16) | 0.93 (0.14) | 6.3 (1.1)    | 1.06 (0.04) | -           |
| Engelmann spruce | 46 (5) | 2.22 (0.21)    | 2.41 (0.25)    | 402 (21)          | 375 (20)          | 7.55 (0.98) | 0.87 (0.10) | 15.6 (2.9)   | 1.88 (0.13) | 1.63 (0.45) |
| Ponderosa pine   | 37 (3) | 1.99 (0.12)    | 1.92 (0.07)    | 435 (14)          | 442 (11)          | 9.24 (0.44) | 1.89 (0.11) | 11.1 (1.7)   | 1.72 (0.22) | 1.19 (0.13) |
| Western larch    | 35 (3) | 1.51 (0.14)    | 1.02 (0.09)    | 509 (21)          | 633 (29)          | 1.85 (0.20) | 1.96 (0.28) | 24.8 (3.3)   | 0.66 (0.02) | 0.32 (0.01) |

Table 3.3. Species-level mean values (standard errors in parentheses) for sap flow and scale factor measurements.  $DBH$  = diameter at breast height (cm),  $m_c$  = sapwood water content ( $\text{kg kg}^{-1}$ ),  $\rho_b$  = sapwood density ( $\text{kg m}^{-3}$ ),  $R_s$  = sapwood depth (cm),  $bark$  = bark thickness (cm),  $V_{h\_max}$  = maximum recorded heat-pulse velocity ( $\text{cm s}^{-1}$ ) extracted from mean diurnal curves (Fig. 3),  $Azim$  = proportion of  $V_h$  recorded at a depth of 2 cm on the east side of a trunk to  $V_h$  at the same depth on the west side,  $Rad$  = proportion of  $V_h$  recorded at a depth of 2 cm to  $V_h$  at a depth of 3.7 cm.  $m_c$  and  $\rho_b$  are reported for core samples removed from radial depths of 0-2 and 2-4 cm.



## Figures

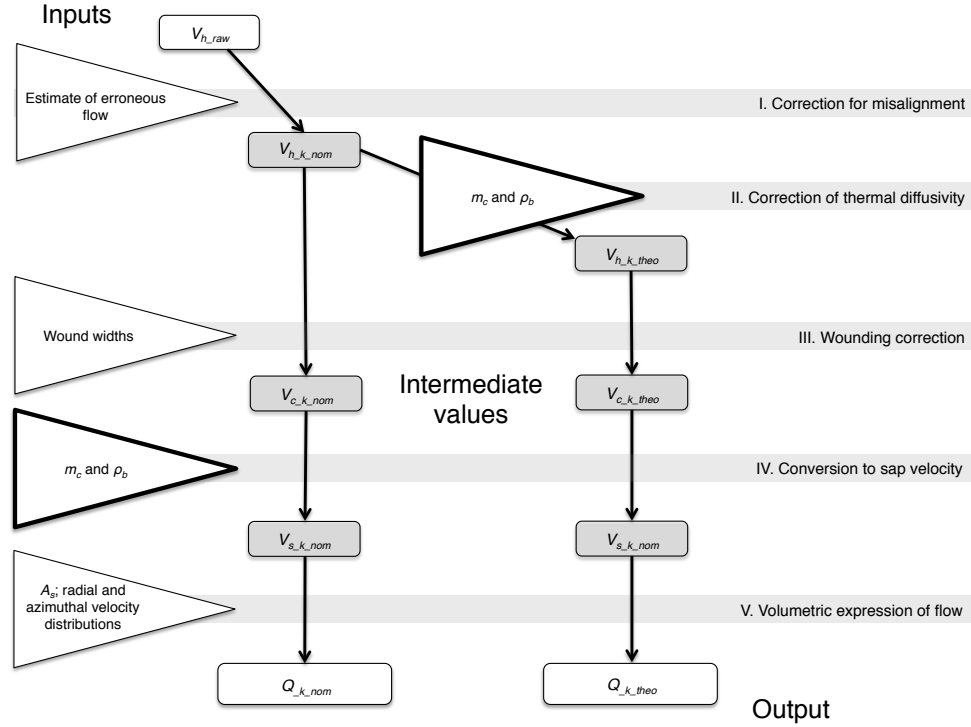


Figure 3.1. Conceptual illustration of the scaling procedure. Scaling heat-pulse velocity ( $V_h$ ) to tree-level transpiration ( $Q$ ) requires auxiliary data sources (in triangles), each of which may contribute uncertainty to the overall estimate of transpiration. Sapwood water content ( $m_c$ ) and density ( $\rho_b$ ) enter the scaling procedure in the calculation of theoretical thermal diffusivity ( $k_{theo}$ , Step II) and in the conversion of  $V_h$  to sap velocity ( $V_s$ , Step IV).

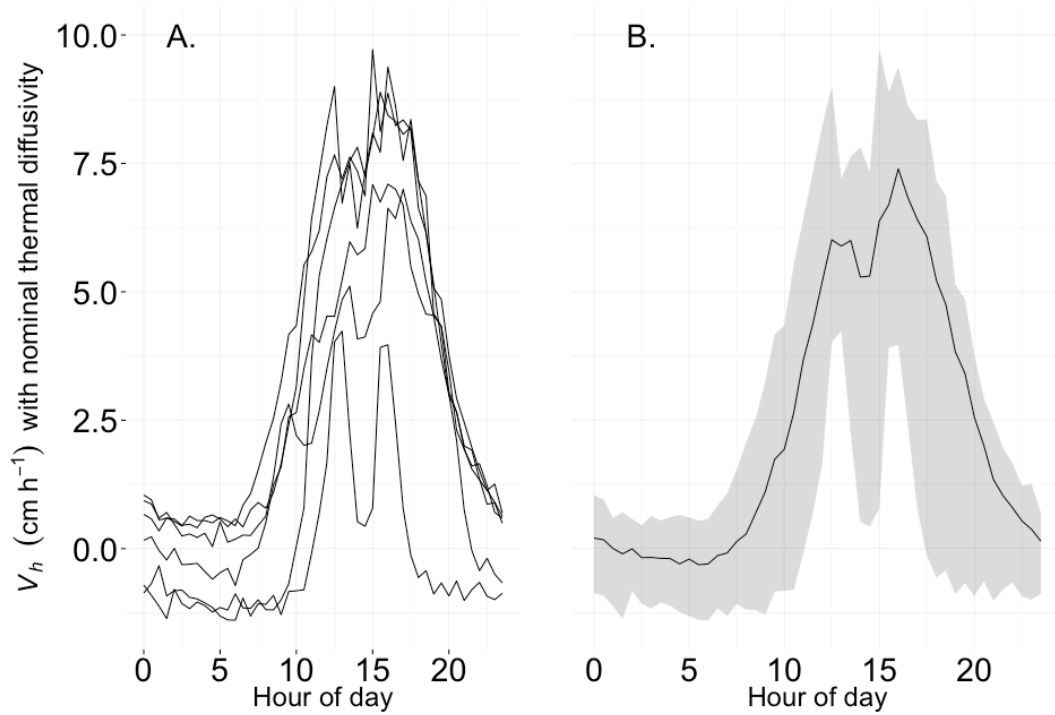


Figure 3.2. Diurnal course of heat-pulse velocity ( $V_h$ , cm h<sup>-1</sup>) recorded at a sapwood depth of 2 cm in an individual tree of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) in May 2014. A. The time course of half-hourly readings of  $V_h$  on six separate days. B. The mean diurnal curve (line) and range of observed time courses (shaded region). The maximum  $V_h$  for each individual was obtained from the mean diurnal curve.

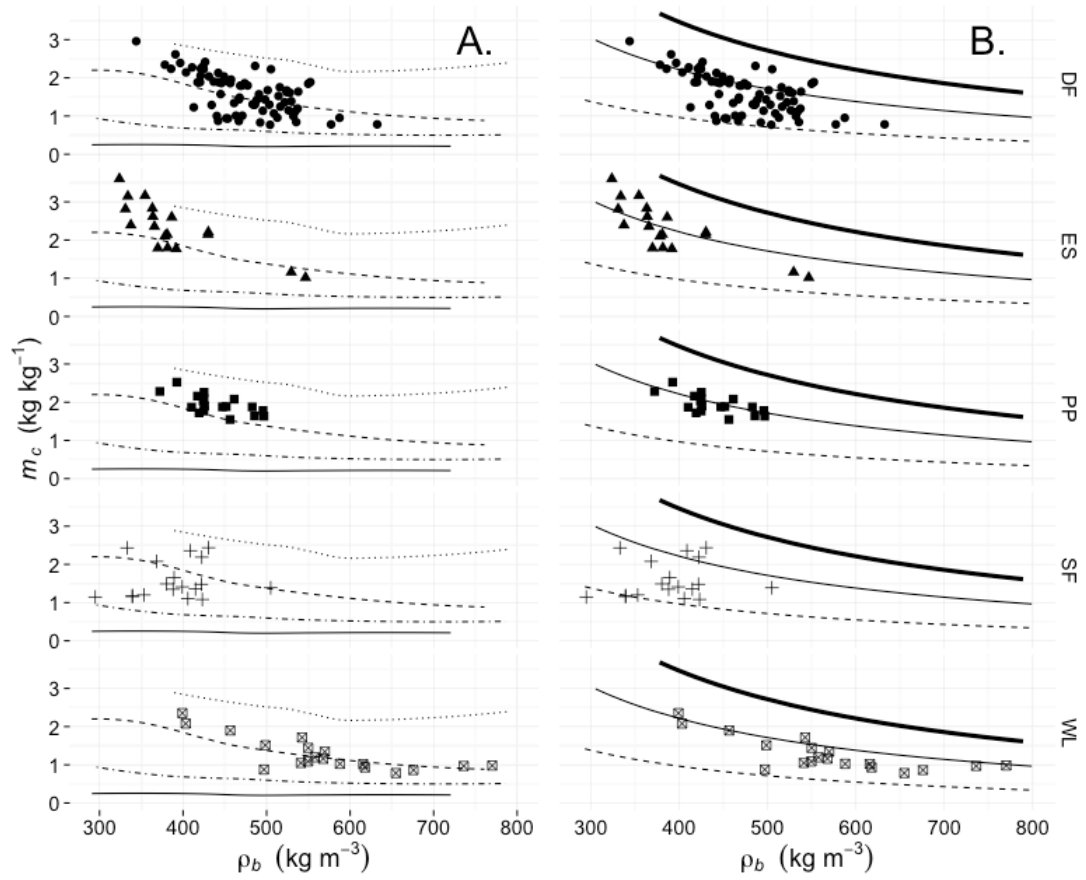


Figure 3.3. Measured sapwood water content ( $m_c$ ) and density ( $\rho_b$ ) from core samples overlaid on isolines of scaling coefficients. A. Lines indicate combinations of  $m_c$  and  $\rho_b$  yielding  $k_{theo}/k_{nom}$  (proportion of theoretical thermal diffusivity, calculated following Burgess et al. 2001, to nominal thermal diffusivity,  $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ ) equal to 0.25 (dotted), 0.50 (dashed), 0.75 (dot-dashed), and 1.0 (solid). B. Lines indicate combinations of  $m_c$  and  $\rho_b$  resulting in  $V_s/V_h$  (proportion of sap to heat-pulse velocities) equal to 0.50 (dashed), 1.0 (solid), and 1.5 (bolded solid). DF = Douglas-fir, ES = Engelmann spruce, PP = ponderosa pine, SF = subalpine fir, WL = western larch.

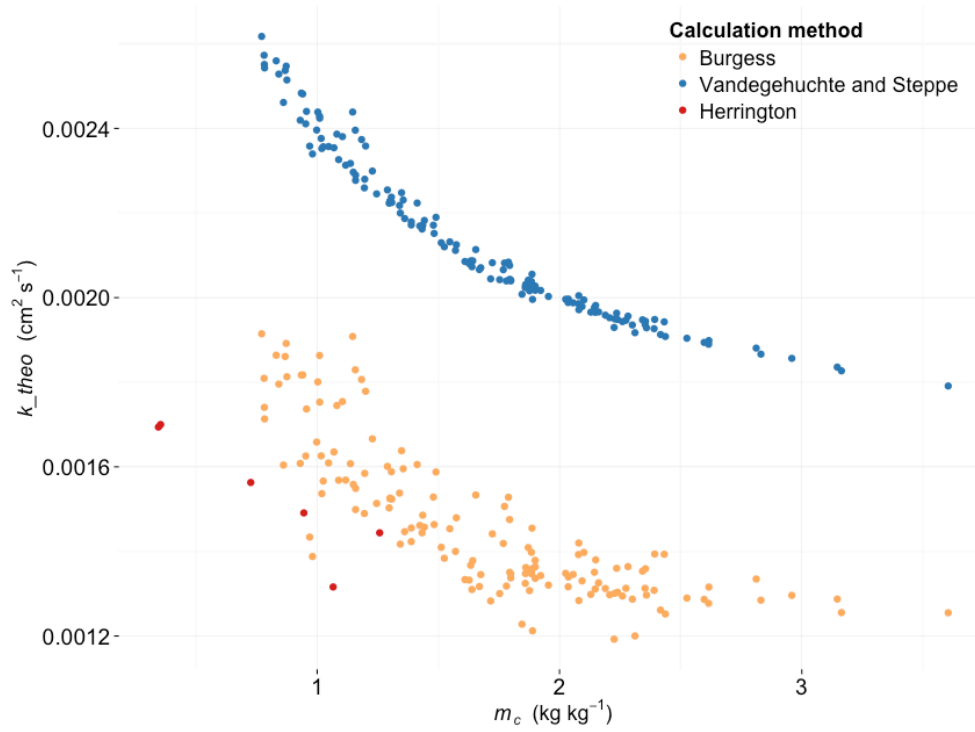


Figure 3.4. Sapwood water content  $m_c$  ( $\text{kg kg}^{-1}$ ) and theoretical thermal diffusivity  $k_{theo}$  ( $\text{cm}^2 \text{s}^{-1}$ ).  $k_{theo}$  was calculated for core samples from all species following the method of Burgess et al. (2001;  $k_{Burg}$ ) and that of Vandegehuchte and Steppe (2012;  $k_{Vand}$ ). Herrington's data (1969) of  $m_c$  and calculated  $k_{theo}$  in red pine are displayed for comparison.

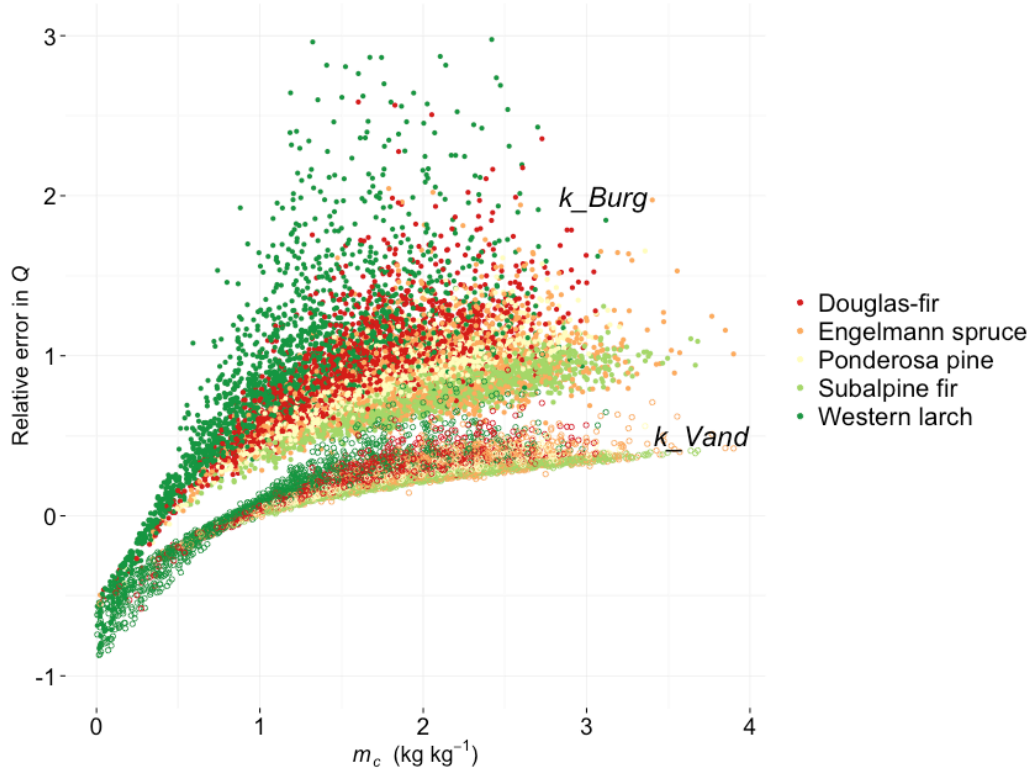


Figure 3.5. Relative error in tree-level transpiration ( $Q$ ) in relation to sapwood water content ( $m_c$ ) from Monte Carlo simulations. Absolute error in  $Q$  was obtained as the difference between  $Q$  as calculated with theoretical thermal diffusivity (a function of  $m_c$  and sapwood basic density,  $\rho_b$ ) and  $Q$  as calculated with nominal thermal diffusivity ( $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ ; Marshall 1958). Relative error is the absolute error divided by  $Q$  calculated with theoretical thermal diffusivity.  $k_{Burg}$  and  $k_{Vand}$  denote thermal diffusivity calculated according to Burgess et al. (2001) and Vandegehuchte and Steppe (2010).

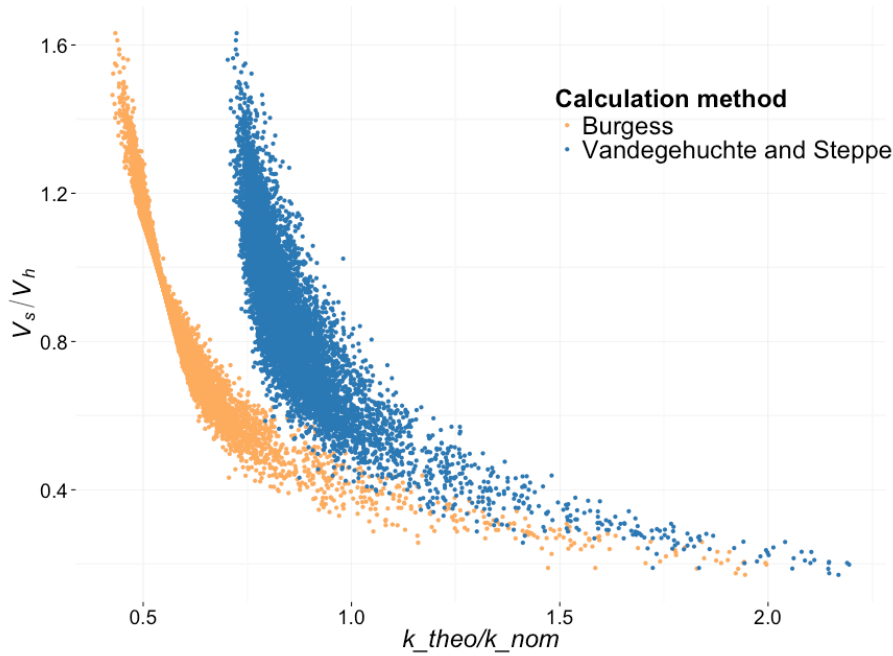


Figure 3.6. Scaling coefficients for simulated trees. x-axis: theoretical thermal diffusivity ( $k_{theo}$ ) divided by nominal thermal diffusivity ( $k_{nom}$ ,  $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ ); y-axis: sap velocity ( $V_s$ ) divided by heat-pulse velocity ( $V_h$ ).

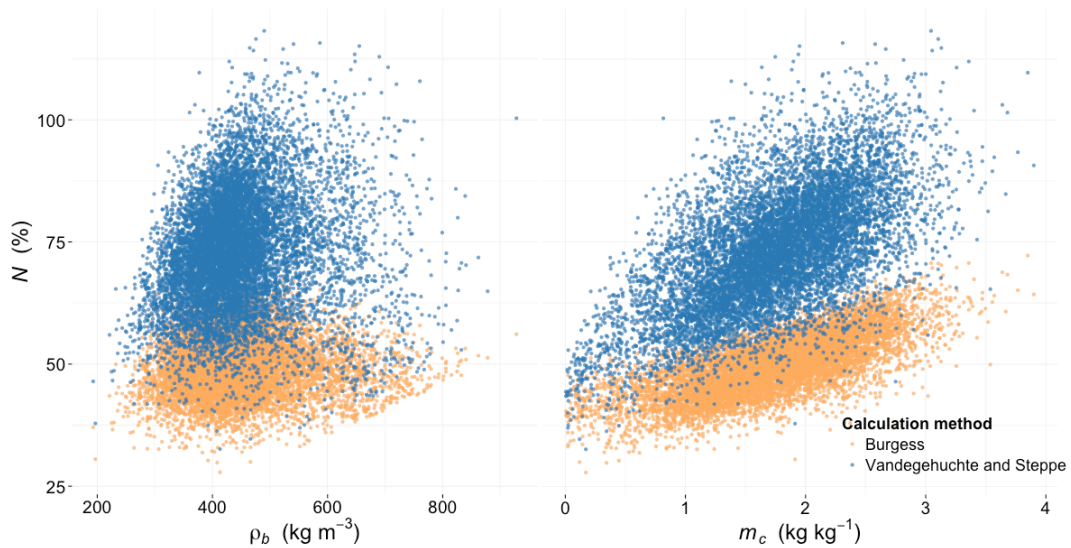


Figure 3.7. Sapwood density ( $\rho_b$ ) and water content ( $m_c$ ) against the net effect ( $N$ ) of substituting theoretical thermal diffusivity ( $k_{theo}$ ) for nominal thermal diffusivity ( $k_{nom}$ ) and converting heat-pulse velocity ( $V_h$ ) to sap velocity ( $V_s$ ). Points indicate output of the simulated scaling procedure, with  $k_{Burg}$  and  $k_{Vand}$  denoting thermal diffusivity calculated according to Burgess et al. (2001) and Vandegehuchte and Steppe (2010).

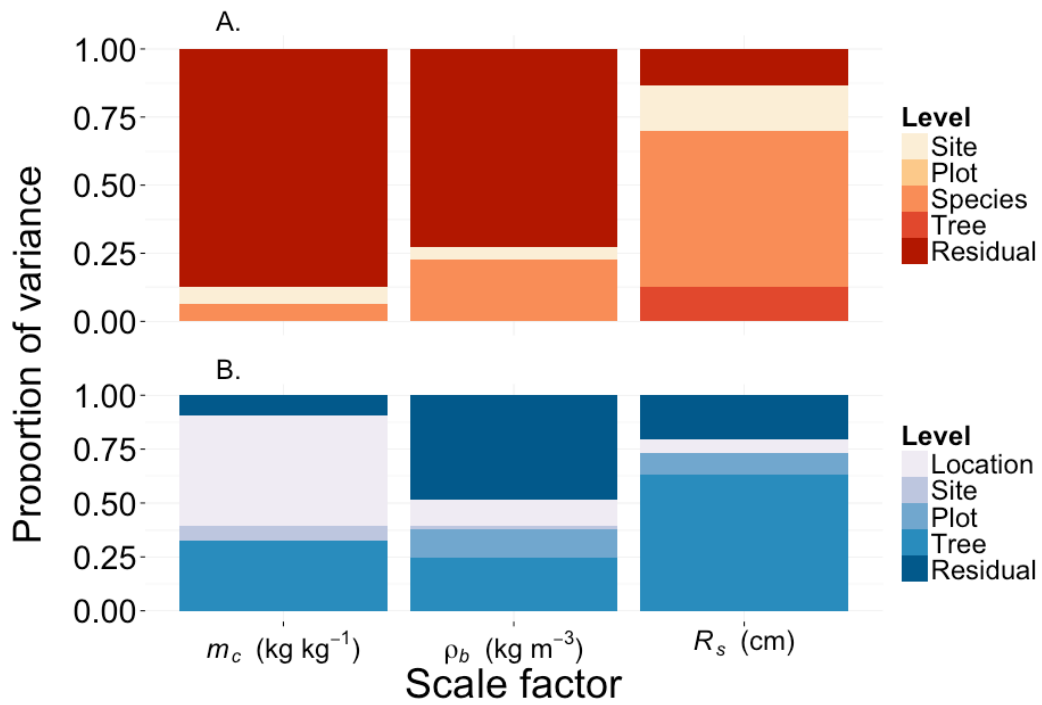


Figure 3.8. Variance in sapwood water content ( $m_c$ ), density ( $\rho_b$ ), and depth ( $R_s$ ) partitioned across sampling levels. A. Interspecific analysis: data from Douglas-fir, ponderosa pine, Engelmann spruce, subalpine fir, and western larch at Lubrecht Experimental Forest (LEF). B. Intraspecific analysis: data from Douglas-fir at LEF and at sites near Bozeman, MT (BZN).

## REFERENCES CITED

- Alvarado-Barrientos MS, Hernández-Santana V, Asbjornsen H (2013) Variability of the radial profile of sap velocity in *Pinus patula* from contrasting stands within the seasonal cloud forest zone of Veracruz, Mexico. *Agric. For. Meteorol.* 168:108–119.
- Angstmann JL, Ewers BE, Kwon H (2012) Size-mediated tree transpiration along soil drainage gradients in boreal black spruce forest wildfire chronosequence. *Tree Physiol.* 32:599–611.
- Beedlow PA, Tingey DT, Waschmann RS, Phillips DL, Johnson MG (2007) Bole water content shows little seasonal variation in century-old Douglas-fir trees. *Tree Physiol.* 27:737–747.
- Burgess SSO, Adams M, Turner NC, Beverly CR, Ong CK, Khan AAH, Bleby TM (2001) An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiol.* 21:1157.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12:351–366.
- Dalsgaard L, Mikkelsen TN, Bastrup-Birk A (2011) Sap flow for beech (*Fagus sylvatica* L.) in a natural and a managed forest—effect of spatial heterogeneity. *J. Plant Ecol.* 4(1-2):23–35.
- Edwards WRN, Becker P, Cermak J (1997) A unified nomenclature for sap flow measurements. *Tree Physiol.* 17:65–67.
- Ellison D, Futter MN, Bishop K (2012) On the forest cover-water yield debate: From demand- to supply-side thinking. *Global Change Biol.* 18:806–820.
- Ford CR, Hubbard RM, Kloeppel BD, Vose JM (2007) A comparison of sap flux-based evapotranspiration estimates with catchment-scale water balance. *Agric. For. Meteorol.* 145:176–185.
- Ghimire CP, Lubczynski MW, Bruijnzeel LA, Chavarro-Rincón D (2014) Transpiration and canopy conductance of two contrasting forest types in the Lesser Himalaya of Central Nepal. *Agric. For. Meteorol.* 197:76–90.
- Goldsmith GR, Matzke NJ, Dawson TE (2013) The incidence and implications of clouds for cloud forest plant water relations. *Ecol. Lett.* 16:307–314.



- Gotsch SG, Asbjornsen H, Holwerda F, Goldsmith GR, Weintraub AE, Dawson TE (2013) Foggy days and dry nights determine crown-level water balance in a seasonal tropical montane cloud forest. *Plant Cell Environ.* doi:10.1111/pce.12151
- Hatton TJ, Greenslade D, Dawes WR (1992) Integration of sap flow velocity in elliptical stems. *Tree Physiol.* 11:185–196.
- Herrington, L.P. 1969. On temperature and heat flow in tree stems. *Yale University School of Forestry Bulletin* 73:1-79.
- Hu J, Moore DJP, Riveros-Iregui DA, Burns SP, Monson RK (2010) Modeling whole-tree carbon assimilation rate using observed transpiration rates and needle sugar carbon isotope ratios. *New Phytol.* 185:1000-1015.
- Jung EY, Otieno D, Lee B, Lim JH, Kang SK, Schmidt MWT, Tenhunen J (2011) Upscaling to stand transpiration of an Asian temperate mixed-deciduous forest from single tree sapflow measurements. *Plant Ecol.* 212:383–395.
- Köstner B, Granier A, Cermak J (1998) Sap flow measurements in forest stands: methods and uncertainties. *Ann. Sci. For.* 55: 13–27.
- López-Bernal A, Alcántara E, Villalobos FJ (2014) Thermal properties of sapwood of fruit trees as affected by anatomy and water potential: errors in sap flux density measurements based on heat pulse methods. *Trees*, 28:1623–1634.
- Magnussen S, Burgess D (1997) Stochastic resampling techniques for quantifying error propagations in forest field experiments. *Can. J. For. Res.* 27:630–637.
- Maku T (1954) Studies on the heat conduction in wood. *Wood Research Bulletin*, Vol. 13. Wood Research Institute, Kyoto University, Kyoto, Japan, 80 pp.
- Marshall DC (1958) Measurement of sap flow in conifers by heat transport. *Plant Physiol.* 33:385–396.
- Markstrom DC, Hann RA (1972) Seasonal variation in wood permeability and stem moisture content of three Rocky Mountain softwoods. *Research Note No. RM-212*. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station, Colo.
- Messier J, McGill BJ, Lechowicz MJ (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecol. Lett.* 13:838–848.

- Muñoz-Villers LE, Holwerda F, Gómez-Cárdenas M, Equihua M, Asbjornsen H, Bruijnzeel LA, Marín-Castro BE, Tobón C (2012) Water balances of old-growth and regenerating montane cloud forests in central Veracruz, Mexico. *J. Hydrol.* 462–463:53–66.
- Schymanski SJ, Or D, Zwieniecki MA (2013) Stomatal control and leaf thermal and hydraulic capacitances under rapid environmental fluctuations. *PLoS ONE*, 8, e54231.
- Simpson, W. and A. TenWolde. 1999. Wood handbook—wood as an engineering material. In Forest Products Laboratory. General Technical Report FPL\_GTR-113. US Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, 463 pp.
- Steinhagen P (1977) Thermal conductive properties of wood, green or dry, from  $-40^{\circ}$  to  $+100^{\circ}\text{C}$ : a literature review. USDA Forest Service, General technical report FPL-9. US Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI, 9 pp.
- Steppe K, De Pauw DJW, Doody TM, Teskey RO (2010) A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. *Agric. For. Meteorol.* 150:1046–1056.
- Stewart CM (1967) Moisture content of living trees. *Nature*, 214:138–140.
- Swanson RH (1983) Numerical and experimental analyses of implanted- probe heat pulse velocity theory. PhD thesis, University of Alberta.
- Vandegehuchte MW, Steppe K (2012) Improving sap flux density measurements by correctly determining thermal diffusivity, differentiating between bound and unbound water. *Tree Physiol.* 32:930–942.
- Vergeynst LL, Vandegehuchte MW, McGuire MA, Teskey RO, Steppe K (2014) Changes in stem water content influence sap flux density measurements with thermal dissipation probes. *Trees*, 28:949-955.
- Zanne AE, Lopez-Gonzalez G, Coomes DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC, Chave J (2009) Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.234>

## CONCLUSION

Though inquisitive minds first entertained the problem of plant water transport generations ago, the bulk of the research that has shaped our mechanistic understanding of plant hydraulics occurred within the past hundred years, and the pace of knowledge generation shows no signs of deceleration. Tandem breakthroughs in process-based modeling and instrumental development suggest that we will become increasingly able to predict how plants (and the ecosystems they sustain) might respond to various types of perturbations. Equipped with such an understanding, we may gain the capacity to design (or restore) living systems that are truly resilient to external perturbations.

Sap flow methods have provided ecophysiological insights from the scale of whole plants to ecosystems. Studies addressing how changes in stand age, structure, and species composition (e.g., with succession or land cover change) modulate ecosystem functioning have imparted clear societal importance to the field. However, many unquestioned assumptions persist in common practice, and we do not necessary know how sensitive our sap flow-based inferences are to uncertainties associated with these assumptions.

In an effort to make a small contribution to the growing rigor of sap flow studies, I conducted the work defining this thesis with the intention of identifying implicit assumptions and striving to understand their purpose and the consequences of their violation. In the second chapter, I used a sap flow dataset to compare the dynamics of tree water use in individuals of five coniferous species growing in contrasting landscape positions and to relate those dynamics to relevant environmental variables. Towards those

ends, I experimented with a wide variety of methodologies, settling on the subset of approaches presented here. I hope that these approaches may prove useful in future research contexts, in particular in efforts to identify physiological signals in sap flow dynamics. In the third chapter, I explored how the variability of sapwood properties within and among my five study species could contribute to uncertainty in transpiration estimates. After measuring sapwood water content and density (and other complementary variables) in contrasting topographic positions and using these data to conduct a simulation, I concluded that the widespread use of a “nominal” value for the thermal diffusivity of wood has the potential to impart large errors (up to 100%) on sap flow-based transpiration estimates. As sap flow methods are occasionally applied in contentious contexts (e.g., to test the efficacy of woody brush clearing on groundwater recharge), such errors could have monetary and/or legal repercussions. With sustained scrutiny of the physical and physiological principles that make sap flow methods work, future researchers may further reduce the uncertainties and limitations of this time-tested approach to estimating transpiration.

## REFERENCES CITED

- Addington RN, Donovan LA, Mitchell RJ, Vose JM, Pecot SD, Jack SB, Hacke UG, Sperry JS, Oren R (2006) Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats. *Plant Cell Environ.* 29:535–545
- Adelman JD, Ewers BE, Mackay DS (2008) Use of temporal patterns in vapor pressure deficit to explain spatial autocorrelation dynamics in tree transpiration, *Tree Physiol.*, 28(4), 647–658.
- Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration. Guidelines for computing crop water requirements. FAO irrigation and drainage paper no. 56. FAO, Rome, 290 pp.
- Andréassian, V (2004) Waters and Forests: From Historical Controversy to Scientific Debate. *J. Hydrol.* 291: 1–27.
- Angstmann JL, Ewers BE, Kwon H (2012) Size-mediated tree transpiration along soil drainage gradients in boreal black spruce forest wildfire chronosequence. *Tree Physiol.* 32:599-611.
- Bates D, Maechler M, Bolker B, Walker S (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, <URL: <http://CRAN.R-project.org/package=lme4>>.
- Beedlow PA, Tingey DT, Waschmann RS, Phillips DL, Johnson MG (2007) Bole water content shows little seasonal variation in century-old Douglas-fir trees. *Tree Physiol.* 27:737–747.
- Bond BJ, Kavanagh KL (1999) Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. *Tree Physiol.* 19:503-510.
- Bond BJ, Meinzer FC, Brooks JR (2008) How trees influence the hydrological cycle in forest ecosystems, in *Hydroecology and Ecohydrology: Past, Present and Future*, eds. PJ Wood, DM Hannah, and JP Sadler. John Wiley & Sons, Ltd, Hoboken, NJ, USA, pp. 7-35.
- Burgess SSO (2006) Measuring transpiration responses to summer precipitation in a Mediterranean climate: a simple screening tool for identifying plant water-use strategies. *Physiol. Plantarum* 127:404–412.

- Burgess SSO, Adams M, Turner NC, Beverly CR, Ong CK, Khan AAH, Bleby TM (2001) An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiol.* 21:1157.
- Callaway RM, Clebsch EEC, White PS (1989) Predicting wood production by canopy trees in forest communities in the western Great Smoky Mountains. *Forest Science*, 35:338–348.
- Carter JL, White DA (2009) Plasticity in the Huber value contributes to homeostasis in leaf water relations of a mallee Eucalypt with variation to groundwater depth. *Tree Physiol.* 29:1407–1418.
- Chouakria-Douzal A, Nagabhushan PN (2007) Adaptive dissimilarity index for measuring time series proximity. *Adv. Data Anal. Classif.* 1(1): 5–21.
- Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment, in *Integration of Activity in the Higher Plant*, ed. DH Jennings. Cambridge University Press, Cambridge, UK, pp. 471–505.
- D’Odorico P, Laio F, Porporato A, Ridolfi L, Rinaldo A, Rodriguez-Iturbe I (2010) Ecohydrology of Terrestrial Ecosystems. *BioScience*, 60(11):898-907.
- Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the role of tree size and hydraulic lift. *Tree Physiol.* 16:263–272.
- Edwards WRN, Becker P, Cermak J (1997) A unified nomenclature for sap flow measurements. *Tree Physiol.* 17:65–67.
- Emanuel RE, D’Odorico P, Epstein HE (2007) A dynamic soil water threshold for vegetation water stress derived from stomatal conductance models. *Water Resour. Res.*, 43, W03431, doi:10.1029/2005WR004831
- Ewers BE, Bon-Lamberty B, Mackay DS (2011) Consequences of stand age and species’ functional trait changes on ecosystem water use of forests, in *Size- and Age-related Changes in Tree Structure and Function*, eds. FC Meinzer, B Lachenbruch, TE Dawson. Springer, Dordrecht.
- Ford CR, Goranson CE, Mitchell RJ, Will RE, Teskey RO (2005) Modeling canopy transpiration using time series analysis: a case study illustrating the effect of soil moisture deficit on *Pinus taeda*. *Agric For. Meteorol.* 130:163–175.
- Ford CR, Hubbard RM, Vose JM (2011) Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. *Ecohydrology*, 4:183–195.

- Gao J, Zhao P, Shen W, Niu J, Zhu L, Ni G (2015) Biophysical limits to responses of water flux to vapor pressure deficit in seven tree species with contrasting land use regimes. *Agric. For. Meteorol.* 200:258-269.
- Ghimire CP, Lubczynski MW, Bruijnzeel LA, Chavarro-Rincón D (2014) Transpiration and canopy conductance of two contrasting forest types in the Lesser Himalaya of Central Nepal. *Agric. For. Meteorol.* 197:76–90.
- Gotsch SG, Asbjornsen H, Holwerda F, Goldsmith GR, Weintraub AE, Dawson TE (2014) Foggy days and dry nights determine crown-level water balance in a seasonal tropical montane cloud forest. *Plant Cell Environ.* doi:10.1111/pce.12151
- Grier CC, Running SW (1977) Leaf area of mature northwestern coniferous forests: relation to site water-balance. *Ecology* 58:893–899.
- Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schäfer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia*, 124:495–505.
- Hernandez-Santana V, Asbjornsen H, Sauer T, Isenhardt T, Schilling K, Schultz R (2011) Enhanced transpiration by riparian buffer trees in response to advection in a humid temperate agricultural landscape. *For. Ecol. Manag.* 261:1415–1427.
- Hu J, Moore DJP, Riveros-Iregui DA, Burns SP, Monson RK (2010) Modeling whole-tree carbon assimilation rate using observed transpiration rates and needle sugar carbon isotope ratios. *New Phytol.* 185:1000-1015.
- Hwang T, Band LE, Vose JM, Tague C (2012) Ecosystem processes at the watershed scale: Hydrologic vegetation gradient as an indicator for lateral hydrologic connectivity of headwater catchments. *Water Resour. Res.* 48, doi:10.1029/2011wr011301.
- Irvine J, Perks MP, Magnani F, Grace J (1998) The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiol.* 18(6):393–402
- Iverson LR, Dale ME, Scott CT, Prasad A (1997) A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.). *Landscape Ecol.* 12:331-348.
- Jencso KG, McGlynn BL (2011) Hierarchical controls on runoff generation: Topographically driven hydrologic connectivity, geology, and vegetation, *Water Resour. Res.*, 47, W11527, doi:10.1029/2011WR010666.

- Jenkins RB, Coops NC (2011) Landscape controls on structural variation in eucalypt vegetation communities: Woronora Plateau, Australia. *Australian Geographer* 42(1):1-17.
- Kopecky M, Cizkova S (2010) Using topographic wetness index in vegetation ecology: does the algorithm matter? *Appl. Veg. Sci.* 13:450-459.
- Köstner B, Falge E, Tenhunen D (2002) Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. *Tree Physiol.* 22:567–574.
- Link P, Simonin K, Maness H, Oshun J, Dawson T, Fung I (2014) Species differences in the seasonality of evergreen tree transpiration in a Mediterranean climate: Analysis of multiyear, half-hourly sap flow observations, *Water Resour. Res.*, 50, 1869–1894, doi:10.1002/ 2013WR014023.
- Lohammar T, Larsson S, Linder S, Falk SO (1980) FAST: Simulation models of gaseous exchange in Scots Pine, in *Structure and Function of Northern Coniferous Forests: An Ecosystem Study*, *Ecol. Bull.*, vol. 32, ed. T. Persson, pp. 505–523, Stockholm, Oikos Editorial Office.
- López-Bernal A, Alcántara E, Villalobos FJ (2014) Thermal properties of sapwood of fruit trees as affected by anatomy and water potential: errors in sap flux density measurements based on heat pulse methods. *Trees*, 28:1623–1634.
- Loranty MM, Mackay DS, Ewers BE, Adelman JD, Kruger EL (2008) Environmental drivers of spatial variation in whole-tree transpiration in an aspen-dominated upland-to-wetland forest gradient, *Water Resour. Res.*, 44, W02441, doi:10.1029/2007WR006272.
- Loustau, D., and A. Granier. 1993. Environmental control of water flux through Maritime pine (*Pinus pinaster* Ait.), in *Water transport in plants under climatic stress*, eds. M. Borghetti, J. Grace, and A. Raschi, Cambridge University Press, Cambridge, UK. pp. 205-218
- Mackay DS, Band LE (1997) Forest ecosystem processes at the watershed scale: Dynamic coupling of distributed hydrology and canopy growth, *Hydrol. Processes*, 11:1197–1217.
- Mackay DS, Ewers Be, Loranty MM, Kruger EL (2010) On the representativeness of plot size and location for scaling transpiration from trees to a stand, *J. Geophys. Res.*, 115, G02016, doi:10.1029/ 2009JG001092.
- Maherali H, DeLucia EH (2001) Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia* 129:481–491.



- Matyssek R, Wieser G, Patzner K, Blaschke H, Häberle K-H (2009) Transpiration of forest trees and stands at different altitude: consistencies rather than contrasts? *Eur J. Forest Res.* 128:579-596.
- McDowell NG, Phillips N, Lunch CK, Bond BJ, Ryan MG (2002) An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiol.* 22:763–774.
- McNab WH (1989) Terrain shape index: Quantifying effect of minor landforms on tree height. *Forest Science*, 35: 91–104.
- McNab WH (1993) A topographic index to quantify the effect of mesoscale landform on site productivity. *Can. J. of For. Res.*, 23:1100– 1107.
- Meinzer F (2003) Functional convergence in plant responses to the environment. *Oecologia* 134:1-11.
- Monteith JL (1995) A reinterpretation of stomatal responses to humidity. *Plant Cell Environ.* 18:357–364.
- Montero P, Vilar JA (2014) TSclust: An R Package for Time Series Clustering. *Journal of Statistical Software*, 62(1):1-43. <http://www.jstatsoft.org/v62/i01/>.
- Moore GW, Bond BJ, Jones JA, Phillips N, Meinzer FC (2004) Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon, USA. *Tree Physiol* 24:481–491.
- Nimlos TJ (1986) Soils of Lubrecht Experimental Forest. Miscellaneous Publication No. 44. Missoula, MT, Montana Forest and Conservation Experiment Station: 36.
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.
- Oren R, Phillips N, Katul G, Ewers BE, Pataki DE (1998) Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. *Ann. Sci. For.* 55:191– 216.
- Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment*, 22:1515–1526.
- Pataki DE, Oren R, Smith WK (2000) Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology* 81:2557–2566.

- Phillips N, Nagchaudhuri A, Oren R, Katul G (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* 11:412–419.
- Phillips NG, Oren R, Licata J, Linder S (2004) Time series diagnosis of tree hydraulic characteristics. *Tree Physiol.* 24, 879– 890.
- Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ (2014) Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. *Ecol. Lett.* 17:82-91.
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Roddy AB, Winter K, Dawson DE (2015) Responses of petiole sap flow to light and vapor pressure deficit in the tropical tree *Tabebuia rosea* (Bignoniaceae). *PeerJ PrePrints* 3:e1252 <https://dx.doi.org/10.7287/peerj.preprints.1017v1>
- Sala A (2006) Hydraulic compensation in Northern Rocky Mountain conifers: does successional position and life history matter? *Oecologia* 149, 1–11.
- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. *Science* 148:339–346.
- Shinohara Y, Tsuruta K, Ogura A, Noto F, Komatsu H, Otsuki K, Maruyama T (2013) Azimuthal and radial variations in sap flux density and effects on stand-scale transpiration estimates in a Japanese cedar forest. *Tree Physiol.* 33:550-558.
- Soetaert K, Petzoldt T (2010) Inverse Modelling, Sensitivity and Monte Carlo Analysis in R Using Package FME. *Journal of Statistical Software*, 33(3):1-28. URL <http://www.jstatsoft.org/v33/i03/>.
- Swanson RH (1983) Numerical and experimental analyses of implanted- probe heat pulse velocity theory. PhD thesis, University of Alberta.
- Tardieu F, Davies WJ (1993) Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants, *Plant Cell Environ.* 16:341–349, doi:10. 1111/j.1365-3040.1993.tb00880.x.
- Tetens VO (1930) Über einige meteorologische. Begriffe, *Zeitschrift für Geophysik.* 6:297-309.
- Thompson S, Harman C, Heine P, Katul G (2010) Vegetation-infiltration relationships across climatic and soil type gradients, *J. Geophys. Res.-Biogeo.*, 115:1–27.

- Thompson SE, Harman CJ, Troch PA, Brooks PD, Sivapalan M (2011) Spatial scale dependence of ecohydrologically mediated water balance partitioning: A synthesis framework for catchment ecohydrology. *Water Resour. Res.* 47, W00J03, doi:10.1029/2010WR009998.
- Traver E, Ewers BE, Macky DS, Loranty MM (2009) Tree transpiration varies spatially in response to atmospheric but not edaphic conditions. *Funct. Ecol.* 24:273–282
- Tromp-van Meerveld HJ, McDonnell JJ (2006) On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale, *Adv. Water Resour.*, 29(2):293 – 310.
- Vandegehuchte MW, Steppe K (2012) Improving sap flux density measurements by correctly determining thermal diffusivity, differentiating between bound and unbound water. *Tree Physiol.* 32:930–942.
- Waring RH, Landsberg JJ (2011) Generalizing plant–water relations to landscapes, *J. Plant Ecol.*, 4(1-2):101–113.
- Wullschleger SD, Meinzer FC, Vertessy RA (1998) A review of whole-plant water use studies in trees. *Tree Physiol.* 18:499–512.
- Zhu AX (2000) Mapping soil landscape as spatial continuua: The neural network approach. *Water Resour. Res.* 36(3):663-677.