ESTIMATING TREE TRANSPIRATION ACCURATELY DEPENDS ON WOOD TYPE AND SPECIES: A STUDY OF FOUR SOUTHERN APPALACHIAn TREE SPECIES

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The measurement of sap movement in trees is a valuable way to estimate forest evapotranspiration, or the return of water vapor to the atmosphere. The accuracy of these measurements is essential to determining forest evapotranspiration. Importantly, forest evapotranspiration is a major component of water budget, and subsequent water lost through this process affects other fluxes such as streamflow and surface water supply. Using a dual thermal dissipation probe system inserted into sapwood, the difference in temperature ($\Delta T$) between the two probes can be related to sap flux density using an empirically derived equation. The universality of the power function coefficients proposed by Granier in this empirical equation has recently come into question regarding different tree species. Notably, Granier's coefficients may not be universal among different wood types and among trees with varying sapwood to heartwood ratios. It has been suggested that each species should be validated before using the universal coefficients. Using four tree species indigenous to the southern Appalachians (Betula lenta, Liriodendron tulipifera, Nyssa sylvatica, Rhododendron maximum), this study estimates sap flux through excised woody stems using two independent methods: gravimetric and thermal dissipation. This study evaluates whether the species differ significantly among each other by comparing aforementioned gravimetric measurements. Replicates of excised stems were selected from trees growing in the Coweeta basin. Our results indicated that three of the four species require coefficients that differ from Granier's (Betula, Nyssa, Rhododendron). Furthermore, there are significant differences between all but two of the species (Liriodendron and Rhododendron). Future studies will focus on testing other major tree species in the southern Appalachians to improve the accuracy of stand-level transpiration measurements.

BACKGROUND

Sap flux density is the movement of water through the vascular system of a tree per unit area per unit time ($J$, g H$_2$O m$^{-2}$ sapwood s$^{-1}$). Sap flux measurements at the tree-level allow scalar calculation of stand-level canopy transpiration ($E$) and stomatal conductance [Tang et al. 2006], allowing estimates of the forest water budget. Other variables in the water budget include stream runoff, interception, change in groundwater storage, and soil evaporation. An understanding of forest water budgets and $E$, are particularly important to mountainous areas with a history of erosion caused by prevalent logging and construction [Mattson and Swank 1989; Meyer and Tate 1983].

Ava Hoffman is a fourth-year distinguished major in Biology. Following graduation, she hopes to pursue a graduate career, applying her knowledge of forest processes to difficult questions regarding natural resource management, conservation, and climate change. This study was conducted during the summer of 2011 through the U.S. Forest Service at Coweeta Hydrologic Laboratory, part of the Long-Term Ecological Research Network. She is profoundly grateful to her advisors, Drs. Steven Brantley and Chelcy Ford, for their wisdom and guidance.
Sap flux density may be measured using a dual thermal dissipation probe system (Figure 1), which, although invasive, causes minimal damage to the tree. Thermal dissipation probes are commonly used within the United States, though other methods such as the heat pulse velocity technique [Čermák et al. 2004; Smith and Allen 1996; Tognetti et al. 2004] may be used as well. In the thermal dissipation system, a heated probe is placed at a fixed distance downstream ("higher" on a living trunk) from a non-heated reference probe. The heated probe measures the temperature of the sapwood as well as the temperature of the water moving around the probe. Water movement cools the probe as heat is removed downstream (hence "thermal dissipation" probe). The non-heated reference probe measures only the sapwood temperature. The difference in temperature (ΔT) between the two probes provides a useful numerical value; it indicates the heat conducted away from the probe due to sap flow, where ΔT decreases as flow increases. In other words, values of ΔT and sap flux (J) vary inversely; this can be observed in a diurnal time series of ΔT and resulting J values (Figure 2).

The relationship between ΔT and J is represented by a power function. Granier [1985, 1987] expressed ΔT as a function of J using the thermal dissipation system, resulting in fitted coefficients to the power function which were deemed ubiquitous, applying to not only all species but all materials (mesh, wood, sawdust, etc.). However, recent studies suggest that probe placement, sapwood anatomy, and wounding may affect the accuracy of Granier's coefficients [Bush et al. 2010; Clearwater et al. 1999; Taneda and Sperry 2008; Wullschleger et al. 2011]. Often yielding an underestimate of J, [Bush et al. 2010; Wullschleger et al. 2011]. As a result, it has been suggested that each tree species be independently validated, and calibrated if needed to account for anatomical differences.

Sapwood varies widely among different species, based on the arrangement of vessels within an annual ring (ring-porous or diffuse-porous), proportion of sapwood to heartwood, and variable J gradients within the sapwood [Ford et al. 2004; Phillips et al. 1996]. Ring-porous species have one or occasionally two years growth of active sapwood (shallower sapwood) whereas diffuse-porous species have multiple years of active sapwood and therefore a greater depth from the outer surface (deeper sapwood) (Figure 3a).

The difference is based on the diameter of the individual conducting elements in the sapwood—xylem vessels. J gradients occur within these classifications of sapwood according to Ford et al. [2004]. Variation within the sapwood may drastically influence measurements of ΔT because the probe measures an average ΔT along the probe. Ideally, probe length should cover the entire sapwood radius. This avoids accidentally contacting non-conductive heartwood (probe is too long) as well as measuring only faster moving sap in the outermost vessels (probe is too short).

The purpose of this study is to measure sap flux density using two independent methods, gravimetric sap flux density (J) and thermal dissipation, of four woody species in the southern Appalachians and compare their derived power function coefficients to those proposed by Granier. Species selected for the study were Betula lenta (BELE), Liriodendron tulipifera (LITU), Nyssa sylvatica (NYSY), and Rhododendron maximum (RHMA). We hypothesized that Granier’s coefficients would be inadequate for providing estimates of J (often underestimating sap flux), and that the fitted coefficients among species would vary.

**METHODS**

Stem samples were gathered in low-elevation sites in the Coweeta basin in Otto, NC. Sites were chosen based ongoing sap flow studies in the basin. Terrain in the area is considered variable: mountainous and often semi-riparian. Five stems of 4.5–5.5 cm diameter were selected from each species. These four species represent >60% of the forest community leaf area, and >70% of stand level E in these sites. These species show variation in amount of heartwood, although all may be classified as diffuse-porous (Figure 3b). LITU and NYSY generally contain lower sapwood to heartwood ratios.

Stems were cut at a length twice the average vessel length for each species to prevent embolism and to ensure that water would flow through vessel end walls. The stem was secured vertically with clamps, and a positive pressure system consisting of a bottomless graduated cylinder was affixed over the bark onto the top of the stem with paraffin wax. A large Erlenmeyer vacuum flask maintained constant water pressure within the graduated cylinder, supplying water through the open end. This system maintained constant hydraulic pressures to force water down through the stem’s vascular system. This system also allowed changes in the hydraulic pressure to achieve faster or slower sap flow through the stem. Three target hydraulic pressure ranges were used: 2–5, 8–12, and 14+ cm. Typically, 20–30 minutes were allowed for flow to equilibrate to each pressure. The positive pressure applied simulated the effect of transpiration (maintained via tension within living trees). Greater hydraulic pressure within the graduated cylinder represented a greater tension via transpiration. Thermal dissipation probes were installed in each stem by drilling holes of appropriate length into the sapwood. The signal output from the probes, ΔT, was logged every 5 minutes using a Campbell CR10X data logger (Campbell Scientific, Logan, UT, USA). At the same intervals, water flowing out of the stem was independently recorded and weighed with a balance (i.e., gravimetric values). Cross-sectional sapwood area was measured on each stem; conductive sapwood was determined by staining with Congo Red dye. Gravimetric values were then converted to volumetric units based on water temperature (g m² s⁻¹).
DATA ANALYSIS

Values of $\Delta T$ collected from the data logger were first converted to the dimensionless quantity $k$, where $\Delta T_m$ is the maximum $\Delta T$ under zero flow.

$$k = (\Delta T_m - \Delta T)/\Delta T$$

The quantity $k$ was then regressed onto $J_s$ using a power function and two coefficients:

$$J_s = ak^b$$

Coefficients were fit using numerical maximum likelihood solutions with the PROCNLMIXED function in SAS (SAS Institute, Cary, NC, USA) described by Peek et al. (2002). We also used Granier's coefficients with $k$ values and compared them to our fitted values on the same stems.

RESULTS AND DISCUSSION

Visual comparison of $k$ to $J_s$ indicates that use of Granier's coefficients will likely yield an underestimate of sap flux density depending on the species (Figure 4). Our analyses indicate that coefficients for BELE, NYSY, and RHMA differed from predictions using Granier's coefficients (all $p < 0.05$); however, coefficients for the power function for LITU did not significantly differ from Granier's coefficients (Figure 5).

Because sap flux density though RHMA stems was slow, we show those values magnified for clarification in Figure 6. Analyses also indicate that most species differ from each other. BELE/LITU, BELE/NYSY, BELE/RHMA, LITU/NYSY, and NYSY/RHMA all showed significant differences ($p < 0.05$) in their respective coefficients. Coefficients for LITU and RHMA did not significantly differ from one another.

Errors in sap flux measurement are likely due to misplacement of the thermal dissipation probes or differences in sapwood anatomy among species. Wide variation in coefficients among species and from Granier's coefficients necessitates a cautious approach if very accurate evapotranspirative measurements are needed. Ideally, all species must be validated before use to determine if Granier's coefficients will yield a suitable estimate.

A Web of Science search on scientific literature citing Granier's original work [1985] shows that this method is quite popular and is increasing in relevance; indeed, it has been cited over 300 times. Granier's coefficients have been used with little criticism in many species in other environments. In species occupying the southern Appalachians, these coefficients provide a more accurate $E$ estimate for LITU than for the other species we evaluated. Our data suggest that Granier's coefficients may yield underestimates for many species. Based on our work for southern Appalachian woody species, species-specific coefficients will yield more accurate estimates of sap flux density than those published by Granier.

Figure 1. Model of thermal dissipation probes. Note the heated probe (red) is upstream of the non-heated probe (silver).

Figure 2. Values of $\Delta T$ (left) and gravimetric sap flux ($J_s$) (right) vary inversely, diurnally. Figure credit to Steven T. Brantley, Coweeta Hydrologic Laboratory.
Future plans include validating and calibrating, if needed, other southern Appalachian woody species. Our methods may also be optimized to include sources of error: minimizing probe contact with heartwood, minimizing wounding/trauma to the probe insertion site, and increasing understanding of sapwood properties and gradients of sap flux density at different sapwood depths. Minimizing probe contact with heartwood yields more accurate measurements, should the Granier coefficients be used. Minimizing wounding/trauma may be the most pressing challenge, as cavitation may cause underestimates of flux. Embolized vessels often close around the wound site.

Effectiveness of sap flux probes on ring-porous species must also be maximized. Ring-porous species, such as *Quercus alba*, can often reach old-growth status in the southern Appalachians and, as such, can contribute substantially to stand-level $E_T$ (Figure 3a). Differences between individuals of the same species should also be examined, as they may vary among different environments or growing conditions (e.g.,

![Figure 3: Staining study of stems used in sap flow measurements; hydroactive sapwood is stained red, nonfunctional heartwood is not stained. (a) Top left, *Liriodendron tulipifera*, a diffuse-porous species, and bottom left *Quercus alba*, a ring-porous species. Yellow boxes indicate sapwood radius. Note the absence of dye where the probe was inserted. (b) BELE (top left), LITU (top right), NYSY (bottom left) and RHMA (bottom right) sapwood, stained red. Note the unstained heartwood in LITU and NYSY. LITU and NYSY generally contain lower sapwood to heartwood ratios.](image)

**Granier Flux = 0.0119*^{1.21}**

![Figure 4: Summary of all species indicated by data points, where $k$ is a unitless quantity based on $\Delta T$, and sap flux density represents independently measured, gravimetric values (J). The solid line represents estimated sap flow based on Granier’s equation and Granier’s coefficients. Note the apparent underestimate of the solid line.](image)

**Figure 4: Summary of all species indicated by data points, where $k$ is a unitless quantity based on $\Delta T$, and sap flux density represents independently measured, gravimetric values (J). The solid line represents estimated sap flow based on Granier’s equation and Granier’s coefficients. Note the apparent underestimate of the solid line.**

**Figure 5: Breakdown of species data points (circles) and Granier estimates (crosses), where $k$ is a unitless quantity calculated from $\Delta T$, and sap flux density represents independently measured, gravimetric values (J). Equations shown in each panel are based on the best-fit coefficients to the observed data. The Granier equation and coefficients are shown above. Note the differences in coefficients. RHMA is also shown with different scale in Figure 6.**

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soils, elevation, slope, or aspect). Influence of growth rate and yearly biomass accumulation might have unforeseen effects on the species’ coefficients.

The results of this study suggest that the coefficients proposed in Granier [1985] are not universally applicable, and that tree species should be independently validated and calibrated, if needed, to avoid errors in $E$ estimates. Differences in xylem anatomy necessitate this tailored approach. Placement of thermal dissipation probes must also be examined to ensure the most accurate coverage of sapwood.

REFERENCES

Water is the commodity in question. Yet we maintain plasticity problems. Critical questions about the ecological economics of these policies are not yet answered. In order to elucidate the framework and, specifically, the diverse economic services generated through private sector policies, an international framework is needed. Specifically, this framework needs to be economically sound.

The article was written by Thomas Coler, a senior at the University of Virginia majoring in environmental science. His areas of academic interest include urban ecology, environmental policy, and natural resource management. In the coming years, he plans to work in the field of environmental policy. He would like to thank Professor [Name] for his guidance and research on this topic. Thomas Coler is pursuing a degree in environmental science at the University of Virginia. His areas of academic interest include urban ecology, environmental policy, and natural resource management. In the coming years, he plans to work in the field of environmental policy. He would like to thank Professor [Name] for his guidance and research on this topic.
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The Oculus

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Editors’ Note

Dear U.Va. Community,

It is with great pleasure that we present to you the Spring 2012 issue of The Oculus: The Virginia Journal of Undergraduate Research. This semester’s edition contains an amazing breadth of research—from plant biology to linguistics to philosophy—and is characteristic of the diversity of undergraduate research conducted by the University’s students and their faculty members. Within, you will discover research of the highest caliber that demonstrates the fine quality of work that U.Va. students achieve when guided by their intellectual curiosity. It is our hope that through the process of reading this issue, you may also be sparked by the same thirst for knowledge that drove these student researchers.

As our first semester as Editors-in-Chief, we have brought several fresh aspects to the journal. By bringing together the academic communities of the entire university, we have emphasized our goal of multidisciplinarity. For the first time in the history of the journal, our editorial board selected the cover design from a diverse array of competitive submissions from the University’s art community, with fourth year architecture student Diana Fang as our winner. We have also added “Lab Notes,” a section to showcase the latest research conducted by students of U.Va.’s scientific community. In addition, we are highlighting the winners of this year’s Undergraduate Research Network Symposium to display an even greater depth of the research projects conducted at the university. All the while, our editorial board has continued the journal’s tradition of maintaining the highest standard in paper evaluation and selection.

This issue could not have been possible without the support of many. The members of our editorial staff devoted several hours each week to evaluate and discuss the paper submissions. We would like to thank them for all of their efforts, and we would like to give a special thank you to the editors who were involved in the layout of the journal and to the members of the Undergraduate Research Network who helped publicize the journal. We would also like to thank the Center for Undergraduate Excellence for their continued support and guidance. Finally, we would like to thank our authors as well as the faculty advisors who guided them through their research, and we would like to thank you for supporting this semester’s issue of The Oculus.

Thank you, and we hope you enjoy the journal!

Sincerely,

Michelle Choi
Co-Editor-in-Chief

Ko Eun “Janet” Shin
Co-Editor-in-Chief