

# Sap flux measurements in wet tropical forests: unique challenges and opportunities

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## **Abstract**

Tropical rainforests often have great tree species and functional diversity, complex age and stand structure, deep active sapwood, and potential factors that reduce transpiration, such as frequent cloud cover and wet leaves. Such factors generate challenges for estimating transpiration from sap flux measurements. In fact, upscaling approaches have rarely been attempted for diverse tropical forests. Thus, the objective of this paper is to build upon past efforts to scale transpiration and optimize strategies for wet tropical forests. Over a five-year period, we instrumented 44 trees with heat dissipation sap flow sensors within a premontane wet tropical rainforest in Costa Rica (5000 mm MAP). Given high diversity, few instrumented trees belonged to the same species, genus, or even family. In a subset of trees, radial profiles across the full range of active xylem were examined. Measurements were scaled to the stand in two plots using sapwood area. In association with extensive micro meteorological measurements, only ~10% of rainfall was transpired from this forested watershed due to persistent low radiation, evaporative demand, and frequent wet canopy conditions. Contrary to temperate trees, we observed minimal flow reductions in deeper sapwood among the largest trees, whose water use amounted to nearly 80% of the total stand water use, even though they contributed less than 15% to total stand basal area. We found that transpiration was suppressed when leaves were wet, even after accounting for lower vapor pressure deficit and reduced solar radiation. Since soil moisture conditions at this site remain continually above deficit levels, flow reversal has been assumed to be minor and thus has not yet been investigated. The driest month on record resulted in higher, not lower, transpiration. Given the high diversity of these forests, herein we propose practical and innovate approaches to group trees by function or degree of canopy exposure. These efforts are critical for accurate scaling of measurements from individual sensors to stands and for improving global land surface models that increasingly partition canopy components to better represent these functionally and structurally diverse ecosystems.

**Keywords:** stand complexity, xylem variation, scaling, energy-limited

## **INTRODUCTION**

Tropical forests are unique and vital ecosystems, covering a large fraction of the globe and accounting for much of the earth's ecosystem fluxes (Malhi and Grace, 2000). The tropics are a challenging and exciting place to work, with a rich history of scientific discoveries (Kritcher, 2011). Yet these ecosystems, particularly in the southern hemisphere, are not as well represented in water and carbon flux observatory networks as northern temperate ecosystems (Oliphant, 2012). Besides remote access, rainforests present additional hurdles for sensor deployment with the use of electronics in wet environments.

Known for their biodiversity, native tropical rainforests are shaped by patch disturbances (Denslow, 1995; Laurance et al., 1998), tight nutrient cycling (Hilton, 1987), and an equatorial warm climate that contribute to high rates of productivity (Schoor, 2003). Rainfall frequently exceeds evapotranspiration demands, resulting in energy-limited, rather

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than water-limited, conditions driving evaporative fluxes for all or most of the year (Moore et al., 2015). Therefore, the factors that drive variation in transpiration in tropical rainforests are uniquely different from those in temperate forests and semiarid savannas.

Here we discuss a set of ideal practices for estimating transpiration from sap flux measurements in wet tropical forests. Although the number of sap flux studies and methodologies has advanced in recent years (Vandegehuchte and Steppe, 2013), we focus on a set of four challenges that are particularly important to address in the wet tropics: 1) species diversity, 2) stand complexity, 3) radial flow variation within the active xylem, and 4) shifts in the critical environmental drivers that determine transpiration variation.

A variety of studies within multi-species forests utilized systematic scaling approaches to partition sap flux among species or other tree characteristics (Cermak et al., 2004; Ewers et al., 2005; Köstner et al., 1998; Moore et al., 2004; Oishi et al., 2008; Oren et al., 1998; Pataki et al., 2000). All of these studies highlight the critical need for careful selection of target trees based on a full assessment of stem, crown and neighboring trees. However, such upscaling approaches have rarely been attempted for diverse tropical forests (Bruijnzeel et al., 2011; Bucci et al., 2008; Horna et al., 2011; Kunert et al., 2015; McJannet et al., 2007). The objective of this paper is to build upon past efforts to scale transpiration and optimize strategies for wet tropical forests.

First, species diversity poses significant challenges for sap flux studies in the tropics, especially in cases where the goal is to characterize entire native forests. Replicates of the same species may not occur at high enough frequency (e.g.,  $n > 10$  tree individuals) to set up study sites to compare among species. Some systems have palms and lianas as well, which require special sensor calibration (Niu et al., 2015; Renninger et al., 2010) due to their distinct anatomical traits (e.g., wood and leaves; Aparecido et al., 2015).

Second, tree selection must take into account stand complexity (McElhinny et al., 2005). Tropical rainforests tend to have more complex vertical leaf and branch distributions (Terborgh, 1985), multiple age cohorts (Vlam et al., 2017), and a mixture of tree types with varying wood properties that impacts hydraulic conductance (Santiago et al., 2004). Tropical trees exhibit a myriad of canopy architectures (Halle et al., 1978), and the light environment within multi-layer tropical canopies leads to a wide range of radiative conditions (Montgomery and Chazdon, 2001). Likewise, boundary layer conditions vary greatly within such complex canopies, which directly affects the driving force for transpiration (Meinzer et al., 1997).

Third, additional challenges emerge when assessing flow variation within individual trees. Xylem characteristics (e.g., wood density (King et al., 2006)) play an important role in growth rates (Bucci et al., 2004), pest resistance (Martin et al., 2013), and maximum hydraulic conductance (Tyree and Zimmerman, 2002), which vary greatly, even among trees with similar growth habits, such as diffuse porous angiosperms. Sapwood depths and trends in sap flux have not been extensively studied in these forests. The lack of a clear heartwood boundary in some tropical species (Aparecido, 2014) make determination of sapwood depth even more difficult. Many tropical species produce latex or other exudates in their sap to repel insects (Martin et al., 2013), which could interfere with sap flux measurements. In addition, many tropical trees form buttresses or other forms of non-uniform cross-sectional growth that must be accounted for in scaling basal area from trees to stands, not only because of their sapwood depth variability, but due to the younger, fast-growing tissues that buttresses possess in relation to the rest of the tree (Woodcock et al., 2000).

Fourth, given the wet climatic conditions, primary drivers of transpiration variation are skewed relative to critical drivers in more water-limited ecosystems where soil moisture tends to act as the primary driver (Moore et al., 2015). Tropical trees can capture diffuse light to optimize growth under cloudy conditions (Montgomery and Chazdon, 2001), but their water use behavior is generally considered a physically-driven process controlled by vapor pressure deficit and net radiation (Loescher et al., 2005). However, field-based measurements of water fluxes in response to varying climate conditions are not widespread in the tropics (Doley et al., 1987; Letts and Mulligan, 2005; Reinhardt and Smith, 2008). Flux towers capture ecosystem scale dynamics, but rainy, foggy conditions interfere with

measurements (Anber et al., 2015), leading to estimated (rather than direct) measures during frequent precipitation events (e.g., Kumagai et al., 2004). Leaves can remain wet for extended periods, yet little is known about how wet leaf conditions affect transpiration (Chu et al., 2014; Gotsch et al., 2014; Ritter et al., 2009).

We draw upon nearly six years of experience with sap-flux sensor deployment at a premontane rain forest site in Costa Rica to address the four challenges outlined above. We present solutions to each challenge as a framework for future sap flux studies throughout similar sites across the wet tropics. Prior results from this work highlight the unique attributes of our site (Aparecido et al., 2016, 2017; Moore et al., 2018).

## **STUDY AREA DESCRIPTION**

Our site is located at the Texas A&M University Soltis Center for Research and Education in north-central Costa Rica near San Isidro Penas Blancas. This premontane tropical rainforest is situated on the eastern slope of the Monteverde range at 500 m elevation. Trees are predominantly semi-deciduous angiosperms with a few occasional palms and lianas. Annual rainfall recorded since 2010 has ranged from 4220 to 5210 mm. The dry season occurs around January to April, when rainfall totals during those months are reduced to about half that of the rainfall during the wet season, but rarely below 100 mm month<sup>-1</sup>. Hence, the modest, yet distinct dry season in this region is typically wet enough that leaves remain on the trees year-around (i.e., tropical semi-deciduous forest). Averaged over the entire year, leaves in the lower canopy are wet 80% of the time and leaves in the upper canopy are wet 25% of the time (Aparecido et al., 2016).

## **CHALLENGES**

### **Challenge 1: species diversity**

The primary purpose of many sap flux studies is to compare water use within one species or between a few co-occurring species (Moore et al., 2004; Moore and Owens, 2012; Siddiq and Cao, 2016; Wullschleger et al., 2001). However, like most natural tropical rainforests, our forest stand was highly diverse; therefore, to reduce potential bias and optimize our estimate of mean sap flux within a stand, we chose to maximize the number of species instrumented. Our solution to the species diversity challenge was to use a systematic approach that encompasses as much species and size diversity as possible. We used basic heat dissipation probes that can be replicated extensively (Aparecido et al., 2016). This was facilitated by a reliable power source at our site in later years when we were able to extend from 32 to 64 sensors running continuously. That site, as described in detail by Aparecido et al. (2016), had 151 trees within a 2200 m<sup>2</sup> stand that was comprised of 53 species from 35 unique families. There were 31 replicates of the most common species, *Carapa guianensis*; *Gymnanthes riparia* had only five, but more typically we found only one representative per species. After measuring diameter-at-breast-height (DBH) and height and categorizing all trees into three size classes based on canopy exposure (e.g., dominant, midstory, and suppressed), trees were selected to represent the widest range of sizes and species. Our final instrument layout included 43 sensors in 26 trees belonging to 17 species, with three replicates of *C. guianensis* and five other species with two replicates each.

### **Challenge 2: stand complexity**

Scientists are called to find order in what may appear to be chaos using systematic approaches. We stratified our sensor deployment by tree size. However, trees in the same diameter class also varied greatly in their crown size and exposure. Therefore, each tree was classified according to their crown architecture (exposure to solar radiation and vertical position in relation to other trees) as suppressed, mid-story, or dominant. Although suppressed trees in the understory made up a large fraction of the total number of tree individuals in the stand, they did not contribute a large fraction to total leaf and basal area. Therefore, our solution to the stand complexity challenge was to select eight or nine “representative” individuals from each size category. We also replicated within trees

according to size, with 1, 2, 3, 4, or 5 sensors tree<sup>-1</sup> in trees with diameters ranging from 7 to ~220 cm diameter. The largest tree diameters had to be estimated or measured above high buttresses. We found that nearly 77% of the water use at the site was contributed by dominant overstory trees, 20% by the midstory trees, and 4% by suppressed trees (Aparecido et al., 2016).

### **Challenge 3: radial flow variation within the active xylem**

Sapwood determination is the first and most critical step for scaling measurements to the stand (Meinzer et al., 2005). We conducted extensive sapwood surveys to characterize sapwood to basal area distribution in our forest. A safranin dye solution was used to help differentiate the active xylem from wood cores obtained using increment borers. We found that active xylem more readily conducts dye through a fresh sample core. We encountered only one tree whose wood was too dense for manual coring (*Pouteria* sp.); and a few other trees were difficult to core because of sticky latex or resin exudates. Our solution was to rapidly remove the borer immediately after the core was extracted to avoid stuck bits. In cases where manual coring encountered difficulties, successful coring was achieved using a power drill adapter. The results of our sapwood survey revealed that many trees had more than 10 cm of active xylem and some had more than 20 cm! Our sensors only extended to 2 cm, so the next step was to characterize flow variation across the radial profile of active xylem. Compared with temperate trees, few studies have looked at flow variation within tropical trees. Our initial findings suggest that tropical trees may have higher flow rates extending deeper into the sapwood. Our solution to the xylem variation challenge was to install sensors deep into the active xylem in a subset of large trees. We then extrapolated those trends to the entire stand on a relative basis using the ratio of flux in the outer xylem and the relative difference in flux at varying depths proportional to the total sapwood depth (Pataki et al., 2011). Preliminary results indicate high interspecific variation of sap flow variation across the xylem and less pronounced reductions in flow with depth than previously reported for temperate tree species (Moore et al., 2018).

### **Challenge 4: distinct environmental drivers**

Our primary science goal was to investigate transpiration under wet canopy conditions (Aparecido, 2017). As such, we expected shifts in the critical environmental drivers that determine transpiration variation. On the one hand, periods of low rainfall produced sunny conditions with higher vapor pressure deficits that should drive up transpiration fluxes. On the other hand, there was a lot of uncertainty about whether these plants were adapted to cope with such conditions. We first evaluated whether our site experienced soil water deficits, so that we could study the threshold conditions that led to plant water stress. The lowest soil moisture values on record were associated with increases, rather than decreases in transpiration, which led us to conclude that soil water deficits were not a major driver at our site. We also evaluated whether trees transpired at night. Our solution was to resolve zero flow conditions on a nightly basis, given that vapor pressure deficit reached zero more than 95% of the nights. Aparecido et al. (2016) reported that transpiration was ~50% lower under wet canopy conditions than dry canopy conditions. We also investigated intermediate conditions when the upper canopy was dry and the lower canopy was wet (“semidry days”). Since wet leaf conditions led to suppressed transpiration, even after accounting for lower vapor pressure deficit and reduced solar radiation (Aparecido et al., 2016), our solution to characterize the distinct environmental drivers at this wet tropical site was to differentiate transpiration during wet leaf conditions. This has important implications for climatic and hydrological modeling.

### **Other challenges and tradeoffs**

We acknowledge the large body of literature that has led to important improvements in sap flux methodologies (Hölttä et al., 2015; Vandegehuchte and Steppe, 2013). We assessed the local conditions at our site to determine strategies to optimize estimates of transpiration given resource constraints. The resulting tradeoffs were that we did not

extensively account for natural thermal gradients (Do and Rocheteau, 2002), non-flow signal determination (Regalado and Ritter, 2007), wounding effects (Wiedemann et al., 2016), flow reversals (Eller et al., 2013; Goldsmith et al., 2013), time lags (Scholz et al., 2007), or non-zero nocturnal fluxes (Alvarado-Barrientos et al., 2015; Rosado et al., 2012). The use of basic heat dissipation probes allowed for greater replication, but instruments reported to be more precise, particularly during low flows (Fuchs et al., 2017), could have been used in a few trees.

Recent studies have indicated that heat dissipation probes may underestimate actual flow velocities (Fuchs et al., 2017). However, Fuchs et al. (2017) acknowledge this problem occurs at much higher flows than we observed in our trees (i.e., 99% of our observations were below 180 cm h<sup>-1</sup>). By necessity, calibration experiments are conducted using smaller stems (Lu et al., 2004; Sun et al., 2012), which likely have more distinct flow gradients across the sensor than we observe in our trees (Clearwater et al., 1999). Furthermore, we have been very careful to ensure good sensor contact with the wood, which is a potential source of error in such underestimates (Do and Rocheteau, 2002).

## OPPORTUNITIES

There are many opportunities for the use of sap flux sensors to characterize transpiration in rainforests in critical regions throughout the tropics, especially in tropical montane forests. These areas are unique and important regions sensitive to climate changes (Bruijnzeel et al., 2011; Bruijnzeel and Veneklaas, 1998). In addition, they are often targeted for conservation policies that protect forested headwater catchments for municipal water supplies (Min-Venditti et al., 2017). There are many unanswered questions about the contribution of tree water use to site water balance that could elucidate impacts of land use changes in these regions. Such efforts are critical for improving accuracy of transpiration estimates when measurements in individual sensors are scaled to the stand. At the watershed scale, projects such as these provide a better understanding of how evapotranspiration is partitioned. It is also critical to differentiate drivers of transpiration unique to these systems, such as leaf wetness, and identify those drivers that best predict transpiration variation. Ultimately, the goal is to improve global land surface models to accurately represent these functionally and structurally diverse ecosystems.

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