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Research paper

Why size matters: the interactive influences of tree diameter distribution and sap flow parameters on upscaled transpiration

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In stands with a broad range of diameters, a small number of very large trees can disproportionately influence stand basal area and transpiration (E_t). Sap flow-based E_t estimates may be particularly sensitive to large trees due to nonlinear relationships between tree-level water use (Q) and tree diameter at breast height (DBH). Because Q is typically predicted on the basis of DBH and sap flow rates measured in a subset of trees and then summed to obtain E_t, we assessed the relative importance of DBH and sap flow variables (sap velocity, V_s, and sapwood depth, R_s) in determining the magnitude of E_t and its dependence on large trees in a tropical montane forest ecosystem. Specifically, we developed a data-driven simulation framework to vary the relationship between DBH and V_s and stand DBH distribution and then calculate Q, E_t and the proportion of E_t contributed by the largest tree in each stand. Our results demonstrate that variation in how R_s is determined in the largest trees can alter estimates up to 26% of E_t while variation in how V_s is determined can vary results by up to 132%. Taken together, these results highlight a great need to expand our understanding of water transport in large trees as this hinders our ability to predict water fluxes accurately from stand to catchment scales.

Keywords: sap flow, scaling, stand transpiration, tropical montane forests.

Introduction

Sap flow techniques have been around for over 80 years (Huber 1932, Granier 1987, Burgess et al. 2001) and are the basis for some of the most frequently cited values of tree- and stand-level transpiration rates (e.g., Wullschleger et al. 1998, Wilson et al. 2001). These methods are unique in their capacity to measure water use from the scale of tissues to whole plants at precise time intervals while logging over extended periods of time, fostering their use in addressing diverse questions across biological and hydrological sciences (e.g., Asbjornsen et al. 2011, Muñoz-Villers et al. 2012, Berry et al. 2016). By allowing measurement and estimation (i.e., upscaling) of water fluxes across spatial and temporal scales, sap flow sensors provide a powerful tool for understanding how transpiration rates change in response to environmental conditions, stand physiology (canopy-scale stomatal behavior) and structure (e.g., age, species and size distribution) across a variety of ecosystems (Schäfer et al. 2000, Köstner et al. 2002, Novick et al. 2009).

It has long been established that the procedure of upscaling sap flow measurements incorporates uncertainty at several points (Vertessy et al. 1997, Cermák et al. 2004, Jung et al. 2011). Generally, this uncertainty arises at two points, when applying velocity measurements to whole-tree water use and when using whole-tree water use to estimate landscape fluxes. A considerable body of work has assessed the former by considering how sap velocity, sapwood depth and wood properties (water content, basic density, thermal diffusivity, xylem wounding) vary within trees (e.g., Burgess et al. 2001, Ford et al.

2004, Alvarado-Barrientos et al. 2013, Looker et al. 2016). These studies have all drawn similar conclusions, that each of these traits can be scaled reliably to whole-tree water use with empirical functions. Unfortunately, a key knowledge gap still remains in assessing the uncertainty introduced when applying estimates of whole-tree water use to landscapes.

One notable study assessed landscape variation. Ford et al. (2007) found that upscaled stand level transpirations from sap flow were 14% lower than water balance calculations and that stand variation in sapwood area and basal area introduced most of this uncertainty. Generally, studies propose strategies to optimally allocate sampling efforts to constrain uncertainty in transpiration estimates (Ford et al. 2007, Kume et al. 2009). This includes, ideally, measurements of sap velocity and sapwood area (or depth) in trees that represent the entire range of species and size distributions in the area of interest (e.g., plot, stand or catchment; Köstner et al. 1998). Across trees within a site, tree-level water use (Q) generally varies most directly in relation to size-related trends in leaf area and/or canopy position (Ryan and Yoder 1997, Čermák et al. 2004; but see Zimmermann et al. 2000); however, in common practice, researchers typically stratify sap flow sampling by selecting trees across a wide range of diameter (DBH, cm) classes (Oren et al. 1999). While great efforts are taken to stratify the sample, stands or landscapes are likely to include species and size classes outside of the sampled distribution. In the absence of alternative methods, measurements of Q in sampled trees are then used to develop an empirical function predicting Q on the basis of DBH in non-instrumented trees in the area of interest (Vertessy et al. 1997, Wullschleger and King 2000, Meinzer et al. 2005, McJannet et al. 2007, Cristiano et al. 2015). Stand level transpiration (E_t, l T^{-1}) can then be obtained by summing estimated Q across all the trees in an area and dividing by that area.

In addition to its applications for upscaling sap flow measurements, the relationship between water transport with tree size has received attention in many foundational studies (Ryan and Yoder 1997). While some researchers have proposed that physiological functioning increases as a quarter-power function of organism (tree) size (West et al. 1997, Enquist et al. 1998, Sperry et al. 2012, Smith et al. 2014), cross-site sap flow studies have indicated that, in some species, sigmoidal (or asymptotic) functions better approximate $Q = f(\text{DBH})$ than do functions by which Q increases indefinitely with DBH (Jiménez et al. 1996, Meinzer et al. 2005, Kallarackal et al. 2013). Asymptotic relationships are further supported by known size-dependence of other biological exchange processes such as photosynthesis and respiration that diminish in larger trees (Yoder et al. 1994, Meir and Grace 2002, Mencuccini 2002, Niinemets 2002). The precise Q–DBH relationship will disproportionately affect predictions of water use in the largest trees.

Several studies conducted in a wide range of forest types have noted that a small number of large trees can transpire the majority of water lost from a canopy (Köstner et al. 1992, Arneth et al. 1996, Martin et al. 2000, Čermák et al. 2004). The disproportionate contribution of large trees to E_t may be driven by ecophysiological or stand phenomena, such as differences in water transport capacity (e.g., wood density, leaf and/or sapwood area), competitive ability for resources and/or crown microclimatic conditions across tree sizes (Barbour and Whitehead 2003, Fernández and Gyenge 2009, Mitchell et al. 2012, Kallarackal et al. 2013). Notwithstanding the plausibility of these biophysical explanations, the dependence of E_t on the water use of individual large trees may also be sensitive to (and possibly exaggerated by) assumptions about how Q increases with DBH; however, to our knowledge, this has not yet been systematically assessed.

In field studies, Q is not measured directly, but rather is estimated using DBH and measured sap flow parameters, namely sap velocity (V_s) and sapwood area (A_s) or sapwood depth (R_s). The use of DBH as the scalar to derive Q introduces autocorrelation between those two variables (Oren et al. 1998, Meinzer et al. 2001). Hence, the form and parameters of the function $Q = f(\text{DBH})$ result from the calculation of Q itself as well as the empirical relationships between DBH and measured sap flow parameters. The parameters V_s, R_s and A_s have been shown to exhibit a wide range of possible relationships with DBH (Meinzer et al. 2001, McJannet et al. 2007), as well as species (Link et al. 2014, Hernández-Santana et al. 2015, Looker et al. 2016), stand density (Benyon et al. 2015) and age (Zimmermann et al. 2000, Köstner et al. 2002). Additionally, climatic and phenological controls on the dynamics of leaf area and stomatal conductance cause V_s to vary from diurnal to interannual time scales (Jarvis 1976, Loustau et al. 1996, McJannet et al. 2007). These factors collectively impart considerable variability in $Q = f(\text{DBH})$ across sites and through time and may mediate the importance of large trees in determining E_t.

In this study, we examined how assumptions about the relationships between DBH and the sap flow parameters V_s and R_s affect estimates of tree- and stand-level transpiration (Q and E_t) and the proportional contribution of large trees to E_t. We used stand structural data and measurements of V_s and R_s (82 trees, 10 species) from four tropical montane forest sites in central Veracruz, Mexico to develop a framework for modeling stand E_t. These data-driven simulations allowed us to determine how variation in the size-dependence of V_s and R_s alters Q and E_t across a range of stand structures. With this approach, we modeled distinct functions by which V_s and R_s could vary with DBH and applied these functions to simulate Q and E_t for simulated DBH distributions constrained by our observations. Due to the nonlinear relationship between DBH and Q, we expected that E_t would increase with stand basal area and that the proportional contribution of the largest tree in each stand to E_t would be tightly related to the proportion of basal area associated with that same tree. Furthermore, we predicted that the magnitude of

E_t and its dependence on the largest tree in the stand would be sensitive to the functional relationships between DBH and V_s and R_s. We tested these predictions in stands with contrasting DBH distributions and using DBH–V_s relationships established during dry, wet and fog seasons over 2 years.

Materials and methods

Study region and description of sites

The study was conducted in tropical montane forests on the eastern slopes of Cofre de Perote volcano located in central Veracruz, Mexico (19°29′N, 97°02′W). All study sites were located at midslope elevations (1200–1500 m) and included three forests and one shade-coffee site. The climate is defined as 'temperate humid' by the Köppen classification modified by Garcia (1988). In the nearby city of Xalapa, the mean maximum annual temperature is 27.1 ± 1.5 °C and mean annual rainfall is 1463 ± 231 mm year^{-1} (100-year record). This climate is highly seasonal with ~80% of rainfall occurring from June to October (henceforth 'wet season'). This wet season is followed by a cool, dry season from November to February characterized by milder temperatures and cold fronts that produce frequent fog events (henceforth 'fog season'). Finally, March–May is characterized by a warm, dry season as temperatures increase for several months before rain begins (henceforth 'dry season').

Soils of the site are Andisols with deep profiles, a silt-loamy texture and high organic matter content with high C/N ratios (Campos 2008). Additionally the soil horizons have high porosity (0.8 to −0.9 cm^3 cm^{-3}), low bulk density (0.2–0.8 g cm^{-3}) and are generally considered nutrient-poor (Alvarado-Barrientos et al. 2014*a*, 2014*b*). Common tree species span diverse genera including *Carpinus*, *Liquidambar*, *Quercus*, *Platanus* and *Alchornea* (Williams-Linera 2002, Williams-Linera et al. 2013).

Forests of this region exist in a patchwork of disturbance regimes that come from historical clearing of lands for agricultural use, selective cutting for timber and natural turnover from tree mortality (Williams-Linera et al. 2002, Muñoz-Villers and López-Blanco 2008). Thus, to encompass this variation, we measured sap flow across secondary forests of three ages (~20 years, ~40 years and ~100 years) and one coffee agroforestry site. Canopy trees from the coffee site were included in this scaling analysis as they comprised all local montane forest species and exhibit similar diurnal patterns of water use as canopy trees from the forest sites. Within each site, eight representative trees across a wide diameter range were selected for sap flow measurements. In total, this included 82 trees (n = 39 for sap velocity, n = 49 for sapwood depth) of species ranging in DBH from 8 to 66 cm (see Table S1 available as Supplementary Data at *Tree Physiology* Online for tree details). The number of trees differed for each seasonal analysis because at one site not all trees were measured during all seasons. Measurements were conducted from January to July, 2014 for the ~100-year-old forest site and from April to August, 2015 and January to March, 2016 for the remainder of the sites.

Sap flow measurements and conversion to sap velocity (V_s)

Transpiration rates were determined using the heat ratio method (HRM) of sap flow (Burgess et al. 2001). This method has been regularly used in this region due to its ability to detect and quantify low and reverse flow rates that occur during fog events (Muñoz-Villers et al. 2012, Gotsch et al. 2014, Alvarado-Barrientos et al. 2013, 2014*a*, 2014*b*, Holwerda et al. 2016). The HRM utilizes three probes, installed perpendicular to the tree trunk, including a heater probe and two sensor probes spaced 0.6 cm in up- and downstream directions from the heater. Each sensor probe was equipped with three fine wire thermocouples spaced at radial depths of 0.5, 1.7 and 3 cm from the base of the probe. In a few smaller trees, only two thermocouples were utilized at depths of 1.1 and 2.2 cm. For some trees in the ~100-year-old forest the time to maximum temperature (T-max) method of Cohen et al. (1981) and modified by Kluitenberg and Ham (2004) was used, as the heat pulse velocities in these trees were higher than those that could be resolved with the HRM method (Holwerda et al. 2016). All sensors were constructed in the Asbjornsen Lab at the University of New Hampshire or in the Holwerda Lab at the Universidad Nacional Autónoma de México using identical construction protocols.

Prior to sensor installation, the bark was removed from the trunk at a height of ~1.3 m for probe insertion directly into the xylem. A metal drill bit guide (ICT International, Armidale, Australia) was mounted onto the exposed area to ensure accurate spacing and that drill holes were as perpendicular to the trunk face as possible. Once holes were drilled, probes were coated in petroleum jelly for conductivity and carefully inserted into the holes. Molding clay was placed around the sensor bases and reflective foam material was wrapped around the tree to avoid heating from direct sunlight. Ten meter extension cables from each sensor set ran to a central datalogging station consisting of a datalogger, multiplexer and an external 12 V battery (CR1000 and AM16/32; Campbell Scientific Inc., Logan, UT, USA). Every 15 min a heat pulse was sent to the heater probe and the change in temperature 60–100 s following the heat pulse of each thermocouple was recorded by the datalogger. In the ~100-year-old forest, raw temperature data were stored for subsequent calculations (Holwerda et al. 2016).

Using the methodology of Burgess et al. (2001), corrections for misalignment and wounding were conducted. Likewise, heat pulse velocities obtained with the T-max method were corrected for wounding following Cohen et al. (1981). For data sets from April to August, 2015, zero flow velocities were obtained by severing the sapwood immediately above and below the sensor sets. This method was consistent with zero flow calculations using the meteorological method to identify conditions likely to have zero or near-zero flow (e.g., Ambrose et al. 2010,

Gotsch et al. 2014). The corrected heat pulse velocities were converted to sap velocities (V_s) using data on density and water content of the sapwood (Marshall 1958, Burgess et al. 2001). The latter were obtained from cores taken from trees located nearby the sample individuals. Small gaps in the data set (less than 3 h) were filled using an autoregressive integrated moving average (ARIMA) model. If days consisted of gaps larger than 3 h, the data were removed from the analysis. Prior to use in the scaling analysis, V_s rates measurements in individual trees were summarized as mean hourly rates across the radial sapwood fraction (average of the V_s values across three depths measured by our HRM sensors) during daytime hours (9:00–20:00 h local time). We summarized V_s in each tree separately for dry, wet and fog seasons.

Sapwood depth measurement (R_s)

Sapwood depths were measured in 49 individuals spanning DBHs from 9.4 to 66 cm across five of the most common species of the region including *Carpinus tropicalis*, *Platanus mexicana*, *Clethra macrophylla*, *Quercus xalapensis* and *Quercus sartorii*. Because of challenges in clearly delineating sapwood boundaries in tropical regions, a range of methods and dyes were used to determine precise sapwood depths in each species. In *Q. xalapensis* and *Q. sartorii*, a 1% solution of bromocresol green in alcohol best presented the sapwood–heartwood boundary, while in *P. mexicana*, a 1% solution of hematoxylin was utilized. In each of these three species, a core was taken using an increment borer at breast height from each tree and brought to the lab for staining. The sapwood–heartwood boundary was carefully accessed under a stereoscope for each individual core. Two species, *C. macrophylla* and *C. tropicalis*, did not show clear delineations with staining in the laboratory and thus field techniques were used. Specifically, a 0.1% solution of indigo carmine was injected into a hole that had been drilled into a sample tree. The sample was left for 2 h with a slight pressure of 0.1 bar. Then a core was taken 4 cm above the injection point from which the sapwood depth could be clearly delineated (Meinzer et al. 2001). Finally, in each sample tree, DBH and depth of bark were also measured to more closely relate sapwood depth and DBH.

Stand structure measurements

Stand structure data were collected by sampling all trees greater than 5 cm in 18 plots, 16 of which were 400 m^2 while an additional two were 113 m^2. Plots spanned the greater tropical montane forest region and were all within an 8 km diameter circle. These additional two plots had different areas because they were pulled from an earlier study with a different sampling design. For each tree, the DBH, estimated height, crown diameter, species identity and GPS coordinates were collected. For individuals that were difficult to identify, branch samples were collected and taken back to the herbarium at the Instituto de Ecología (Xalapa, Mexico) for identification. Similar to sap flow measurements, plot data were collected across 18 forested sites of various ages (six in mature forest, four in ~40 year old forest, four in ~20 year old forest and four in shade coffee forest) within the region to capture a representative set of size and species distributions within the region. Stand structure metrics obtained from different sized plots are presented on a per-hectare basis for standardization.

Tree- and stand-level sap flow simulations

A simulation exercise was conducted to assess how the relationships between sap flow parameters (V_s and R_s) and DBH affect tree- and stand-level transpiration rates (Q, l h^{-1}), and E_t, mm h^{-1}, respectively) across a range of DBH distributions. The exercise consisted of two sets of procedures: generation of DBH distributions within stands and simulation of sap flow parameters for each tree as a function of its DBH. For each of 1000 iterations, a 400-m^2 forest plot was simulated, in accordance with our stand structure sampling design. The number of individual trees in each plot (N) was sampled from a uniform distribution from 5 to 85, resulting in a stand density that ranged from 125 to 2125 trees ha^{-1}. We simulated the DBH distribution of each stand by drawing N samples from a three-parameter Weibull distribution (Bailey and Dell 1973, Aucoin 2015). Shape and location parameters of the Weibull distribution function were fixed to 1 and 5, respectively, so that simulated values fell within a realistic range of DBH. To approximate the density–diameter relationships observed in real forest stands (e.g., Zeide 1995), we imposed a negative relationship between the scale parameter of the distribution function and N, resulting in an inverse relationship between N and mean DBH and an asymptotic relationship between N and stand basal area (see Figures S1 and S2 available as Supplementary Data at *Tree Physiology* Online).

For each of the simulated DBH distributions, we tested the stand-level consequences of assumptions about how R_s and V_s vary with DBH. We simplified the representation of sap flow-related variables (e.g., by assuming a circular stem cross-sectional area and disregarding radial variation in V_s) in order to evaluate how methodological decisions affect the magnitude of E_t and its dependence on a small number of large trees. To estimate sap flow (Q) for each tree, R_s was predicted on the basis of DBH or as a proportion of the sapwood depth (described in more detail in the following paragraph). Then, V_s was multiplied by the cross-sectional ring corresponding to the radial fraction measured by the sensor (with sensor depth equal to 0.5, 1.7 and 3 cm, depending on R_s). Next, assuming that V_s declined linearly from the tip of the sensor to the sapwood–heartwood boundary, the fraction of sapwood area beyond the tip of the sensor was multiplied by the value of V_s estimated for the point halfway between the tip of the sensor and R_s. The sum of the two products yields Q, which is equivalent to whole-tree transpiration under conditions of steady-state water use; the sum of Q for trees within a stand is taken as stand-level transpiration (E_t). The estimates of E_t were then compared relative to two

theoretical values of evapotranspiration. First, we compared E_t to net radiation, which can be considered as the absolute maximum available energy for E_t. Secondly, transpiration in these humid tropical forests is typically 70–80% of net radiation and thus we used 80% of this value as another point of comparison (Holwerda et al. 2016). Net radiation was estimated from measured shortwave radiation and assuming a fixed albedo of 0.12. Furthermore, net longwave radiation was estimated by multiplying black body radiation at air temperature by a net emissivity factor (calculated from actual vapor pressure) and by a cloudiness factor (calculated from observed shortwave radiation and estimated clear-sky radiation) (Holwerda et al. 2016). While these estimates provide an approximation of potential water use, we acknowledge that there is no direct measure of evapotranspiration (e.g., eddy covariance).

Using these methods to calculate Q and E_t for each simulated stand, we conducted two complementary analyses, focusing separately on how E_t is affected by the relationships between DBH and R_s and V_s. First, we compared two approaches to predicting R_s (and thus A_s) on the basis of DBH. The first model assumed that R_s increased linearly with DBH (Figure 1A; Meinzer et al. 2001), whereas the second model assumed a linear relationship between DBH and R_s as a proportion of the trunk radius (sapwood fraction, $P_s = R_s/(\mathrm{DBH}/2)$, Figure 1B). Both models were fit as quantile regressions (Koenker 2016), with the response variable (P_s) defined as the median value at a particular DBH. Quantile regression was chosen over simple linear regression after we detected non-homogeneous variance in measured P_s across the DBH range (Figure 1B); this change in spread can be represented as an envelope of P_s values by including upper and lower quantiles (2.5th and 97.5th percentiles) in the model. After using these regressions to obtain median R_s, A_s was calculated as the difference between tree basal area ($\pi * (\mathrm{DBH}/2)^2$) and heartwood area ($\pi * (\mathrm{DBH}/2 - R_s)^2$) (Figure 1C). Differences in E_t resulting from these two R_s scaling scenarios were assessed by first calculating Q for each simulated tree using the median value of V_s (i.e., ignoring DBH effects on V_s), summing Q to obtain E_t and then subtracting the E_t value

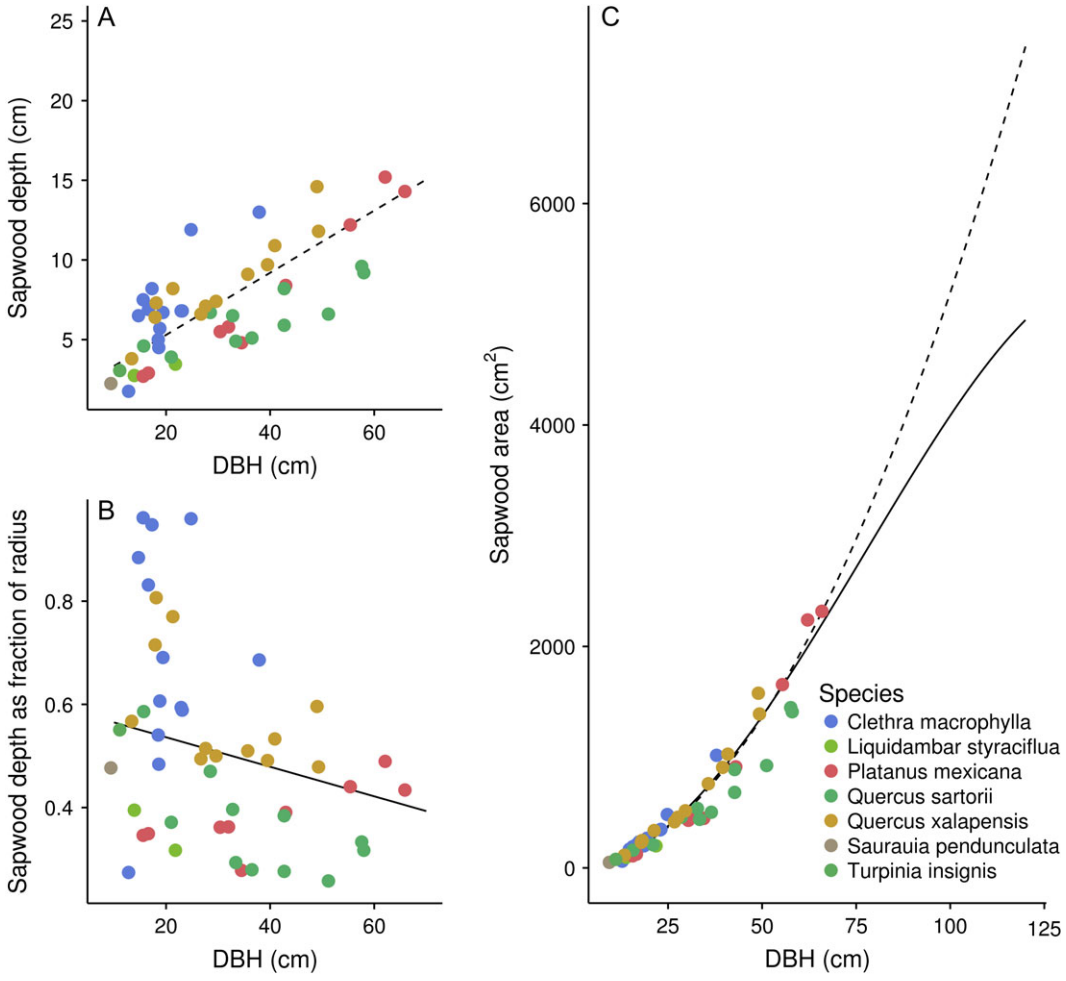

Figure 1. Relationship between sapwood depth and DBH (A) and sapwood depth as a fraction of the radius and DBH (B). Data points are derived from all trees in the study and lines represent best fit regressions. Panel (C) represents total sapwood area by DBH for all trees with dotted and solid lines representing the extrapolation from the best fit lines in (A) and (B).

from the scenario in which P_s scales linearly with DBH from the scenario in which R_s scales linearly with DBH. This difference was also expressed as a relative error by dividing by the E_t value from the P_s scenario (generally the more conservative value). We also calculated the difference in the proportion of E_t contributed by the largest tree within each stand for both scaling scenarios.

The second set of analyses addressed the scaling of V_s with DBH. Previous studies have noted a wide range of possible relationships between DBH and V_s, from null to either positive or negative (Meinzer et al. 2001, McJannet et al. 2007). We detected a positive relationship between DBH and mean hourly V_s across seasons (Figure 2), largely driven by species changes across the DBH range. Because we were concerned with stand-level patterns regardless of the underlying mechanisms (e.g., species, canopy position, etc.), we fit quantile regressions to predict median V_s for all trees during each season as a function of DBH (Figure 2, Table 1). Taking the case of linear scaling of V_s with DBH as an upper limit to Q and E_t, we considered a series of alternative scaling scenarios in which V_s would remain constant above a particular value of DBH (successive 10 cm; horizontal lines in Figure 2). We included this piecewise scaling to quantify the possible errors in E_t (and its dependence on large trees) if the $Q = f(\text{DBH})$ is established with the implicit assumption that V_s can increase indefinitely with tree size. As with the R_s scaling scenarios, we calculated the difference in E_t and the proportion of E_t contributed by the largest tree across all scenarios, normalizing the difference between the E_t values obtained from linear and piecewise scenarios relative to the piecewise scenario values. All simulations and analyses were conducted in R version 3.3.2 (R Development Core Team 2016).

Results

Characterizing relationships between DBH and sap flow parameters

To characterize the scaling relationships between tree diameter (DBH) and sap flow parameters, quantile regressions were

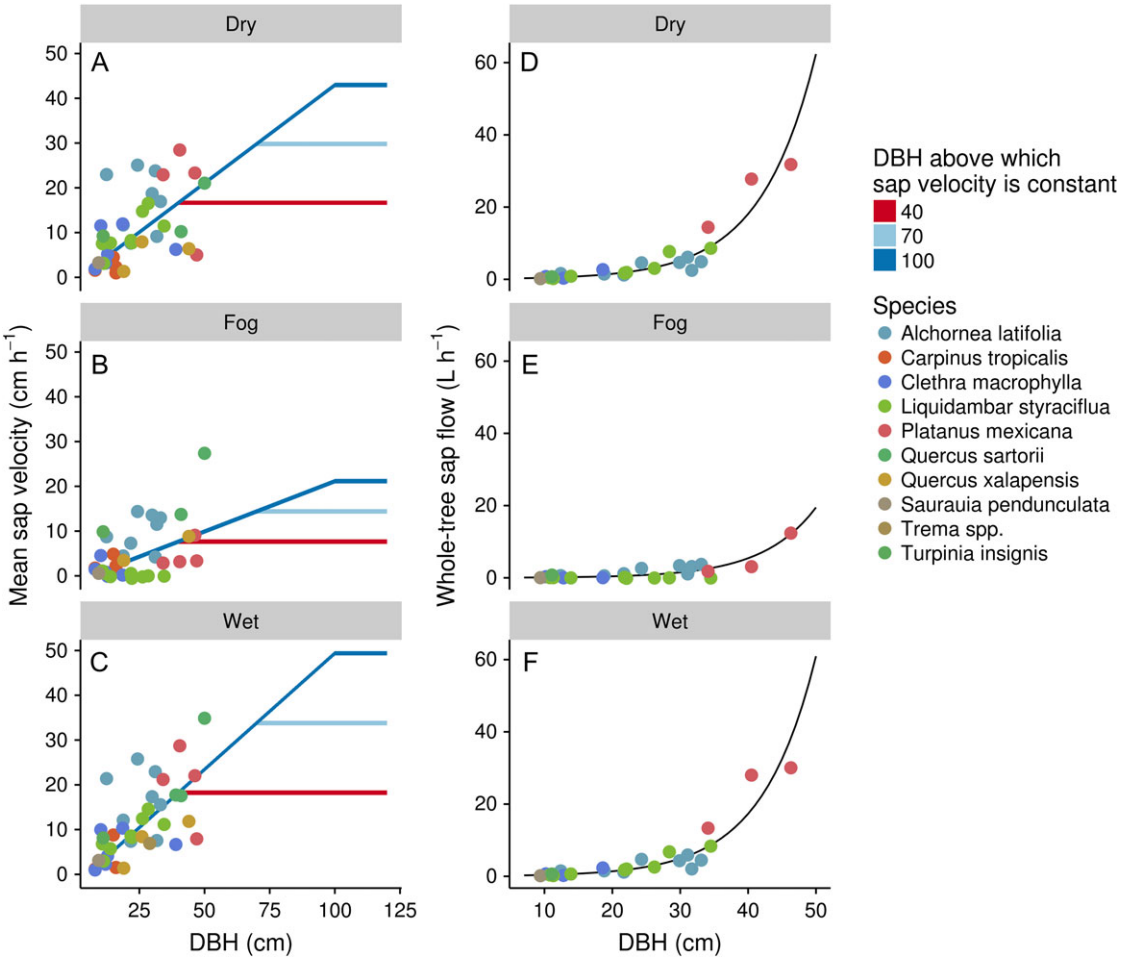

Figure 2. Mean sap velocity by DBH for all trees in the study from dry (A), fog (B) and wet (C) seasons. The initial solid line represents the best fit linear regression. Horizontal lines at subsequent points represent the range of possibilities examined within the subsequent modeling simulations. We assumed that V_s would not linearly increase forever and thus tested each of these points where values might asymptote. The specific colored lines (red, light blue, dark blue) represent asymptotes at 40, 70 and 100 cm DBH and correspond to the same colors used in Figure 4. Panels (D–F) represent the scaling to whole-tree Q assuming that the linear relationships to the left are true across all three seasons, which gives an exponential output.

Table 1. Quantile regression models predicting median value of sap flow parameters (P_s: sapwood depth as a fraction of tree radius; R_s: sapwood depth in cm; V_s: sap velocity in cm h^{-1}) as a function of DBH. Regression coefficients were estimated using the quantreg package (version 5.29) in *R* (version 3.3.2), with standard errors approximated through a bootstrap procedure. These models were fit to data pooled across species and sites ($n = 49$ trees for R_s and P_s; $n = 39$, 35 and 37 trees for V_s during wet, fog and dry seasons, respectively).

Model	Parameter	Value	Std error	*t*-value	*P*-value
Ps	(Intercept)	0.593	0.060	9.721	<0.001
Ps	DBH	−0.003	0.002	−1.481	0.145
Rs	(Intercept)	1.390	1.297	1.072	0.289
Rs	DBH	0.195	0.045	4.298	<0.001
Vs_wet	(Intercept)	−2.520	2.638	−0.955	0.346
Vs_wet	DBH	0.519	0.125	4.158	<0.001
Vs_dry	(Intercept)	−0.862	3.068	−0.281	0.781
Vs_dry	DBH	0.438	0.164	2.667	0.011
Vs_fog	(Intercept)	−1.326	1.592	−0.833	0.411
Vs_fog	DBH	0.225	0.104	2.163	0.038

performed between DBH and sapwood depth (R_s), sapwood depth as a fraction of radius (P_s) and sap velocity (V_s; Figures 1 and 2, Table 1). There was a significant positive relationship between R_s and DBH after accounting for species-specific intercepts ($P < 0.001$), highlighting that mean sapwood depth generally increased with increasing DBH within the range of sizes sampled (Table 1, Figure 1A). We also detected a negative relationship between DBH and P_s (Figure 1B). These two distinct approaches to modeling the relationship between DBH and sapwood depth (i.e., R_s or P_s scales linearly with DBH) led to divergent estimations of total sapwood area for trees. When sapwood area was calculated with R_s, sapwood area scaled exponentially with DBH, whereas the use of P_s led to a sigmoidal relationship (Figure 1C). As with P_s, V_s varied significantly with DBH only when species were pooled ($P = 0.0018$ for slope coefficient in simple linear regression of dry-season V_s compared with $P = 0.414$ for model with species-specific intercepts). These findings were consistent across all three seasons in the study region (Figure 2), with reduced sap velocities during the fog season leading to an apparent decrease in slope (0.426 cm h^{-1} cm^{-1} in the wet season, 0.311 cm h^{-1} cm^{-1} in the dry season and 0.249 cm h^{-1} cm^{-1} in the fog season), again explained by species differences.

Characterizing plot diversity, size distributions and influence on stand transpiration

Eighteen plots were sampled for size and species distributions to assess variation in multiple variables across the plots (Figure 3). The number of stems in a plot ranged from just 5 trees to 117 trees and the DBH of the largest tree in a plot ranged from 29 to 109 cm. To determine the relative influence of tree diameters on stand structural metrics (namely, basal area) and total stand transpiration, the percentage contribution of each tree size class to stand-level estimates was derived. Most plots were dominated by trees smaller than 30 cm DBH (Figure 3A–C). When comparing the distribution of tree diameters across increasing plot basal area, there was a general trend towards a greater number of larger single trees and fewer smaller trees (from A to C in Figure 3). The percentage of transpiration coming from each size class followed a less consistent pattern with the largest influences typically coming from medium or larger trees. The largest influence of one size class typically occurred above 40 cm DBH and often in trees above 70 cm DBH (Figure 3D–F). Equally important, the absolute value was often larger for the peak values with the most important size class typically predicting well over 50% of the plot transpiration from a single size class. These size distributions were used as a base for developing a set of plot distributions in the simulation exercises.

Stand sap flow simulations

The scenarios concerning the scaling of sapwood depth with DBH yielded qualitatively different conclusions from the scenarios involving sap velocity. The two sapwood depth scenarios (i.e., with either R_s or P_s scaling linearly with DBH) resulted in estimates of E_t that diverged by up to 0.1 mm h^{-1}, or 26% of E_t as estimated in the DBH–P_s scenario. For V_s, the difference between the two extreme scenarios (V_s scaling linearly with DBH versus remaining constant above 40 cm DBH) produced estimates of E_t that diverged up to 0.78 mm h^{-1}, or 132% of E_t. When plots had trees larger than 40 cm DBH, the slope of the relationship between stand transpiration and basal area was steeper across all three seasons (Figure 4, Table 1). Specifically, the stand transpiration estimates surpassed the constrained theoretical upper limits derived from the maximum available energy for E_t (Figure 4, solid and dotted horizontal lines). For stands with large trees, all estimates were greater than the maximum available energy when sap velocity was allowed to increase until 100 cm DBH. When sap velocity was held constant at lower DBHs (e.g., 40 cm), this maximum was reached only at high stand basal areas. For ease of demonstration, only simulations where sap flow was held constant above 40, 70 and 100 cm DBH are shown in Figure 4.

We further considered the influence of the largest tree to stand transpiration rates relative to stand basal area (Figure 5). When allowing V_s to vary based on the DBH where sap flow was held constant produced significant variation in the contribution of the largest tree to stand transpiration (Figure 5, left). Importantly, the majority of these values fell above the default 1:1 line meaning that the contribution of the largest tree to stand transpiration is greater than the contribution to basal area. When V_s was held constant and R_s allowed to vary, results were much more consistent and fell near the 1:1 line meaning that variation in R_s had less influence on the contribution of large trees to stand transpiration. Finally, a comparison of the stand level outputs when V_s or R_s were allowed to vary while the other was held

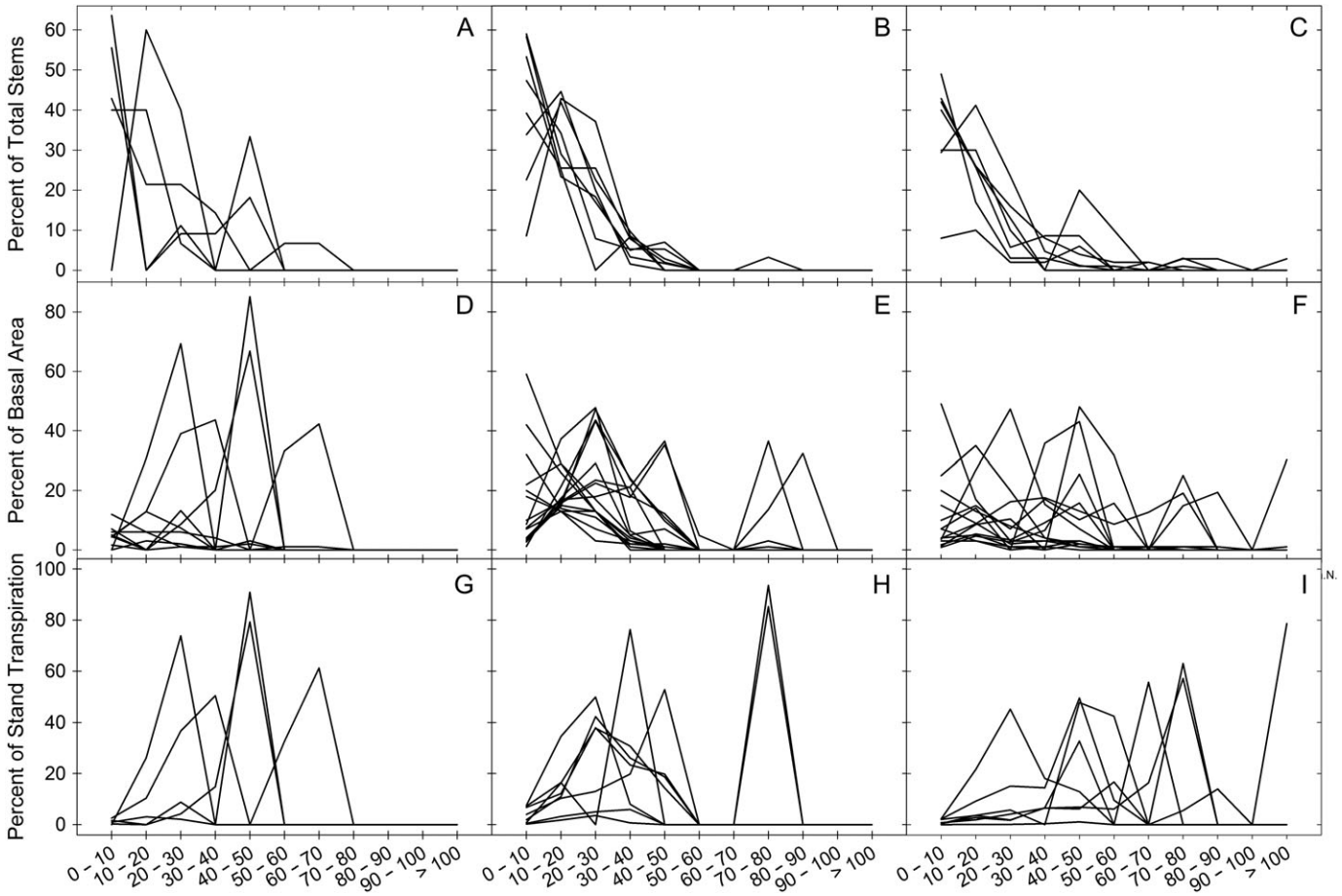

Figure 3. The percentage of stems (A–C), percentage of stand basal area (D–F) and percentage of stand transpiration (G–I) from each size class binned in 10 cm groups. Plots are separated into those with total stand basal areas below 20 m^2 ha^{-1} (A, D and G), 20–40 m^2 ha^{-1} (B, E and H) and greater than 40 m^2 ha^{-1} (C, F and I). Generally transpiration skews disproportionately towards medium and larger size classes while the proportion of stems skews towards lower size classes.

constant produced high variation in their outputs depending on the DBH sap velocity that was held constant (Figure 6). As expected, the variation between the groups was reduced if the constant DBH was very high (e.g., 100 cm DBH).

Discussion

Our results demonstrate that fundamental assumptions about the empirical relationships between sap flow scalar parameters and tree size can have a significant impact on tree- and stand-level estimates of water fluxes (Q and E_t, respectively). Modeling exercises exploring a broad range of stand structures (i.e., stem density and DBH distributional characteristics) revealed how the scaling of sap flow parameters (sapwood depth and sap velocity, R_s and V_s) with DBH gives rise to distinct relationships between stand basal area and E_t (Figure 4). Importantly, this means that E_t cannot be accurately predicted on the basis of stand structure and basal area alone. At a given basal area, estimates of E_t diverged by up to 132% depending on how V_s was assumed to scale with DBH, while the R_s scenarios diverged by up to 26%. In addition to these differences in E_t, our modeling results indicated that the largest trees in a plot can contribute the majority of E_t (e.g., 98% when the largest tree is 4.4 times greater than the median DBH and stem density is low) and that the magnitude of that contribution also depends on the scaling of sap flow parameters with DBH (Figures 5 and 6). Taken together, these findings underscore the need for more targeted characterization of sap flow parameters and quantification of water transport in large trees, which hinder predictions of landscape water fluxes.

Though we were unable to measure R_s and V_s in the largest trees in our study sites, we argue that the plausible envelope of these variables across the range of DBH can be constrained using available field data and by considering the physical limitations on water transport. At the stand level, we estimated a maximum value of potential E_t for each season if evapotranspiration were limited only by net radiation (i.e., zero hydraulic, stomatal, boundary layer resistances, and zero turbulent and storage fluxes of sensible heat). Estimates of E_t were greater than net radiation when V_s was held constant at 100 cm DBH. Additionally, when V_s was held constant at lower DBHs, this

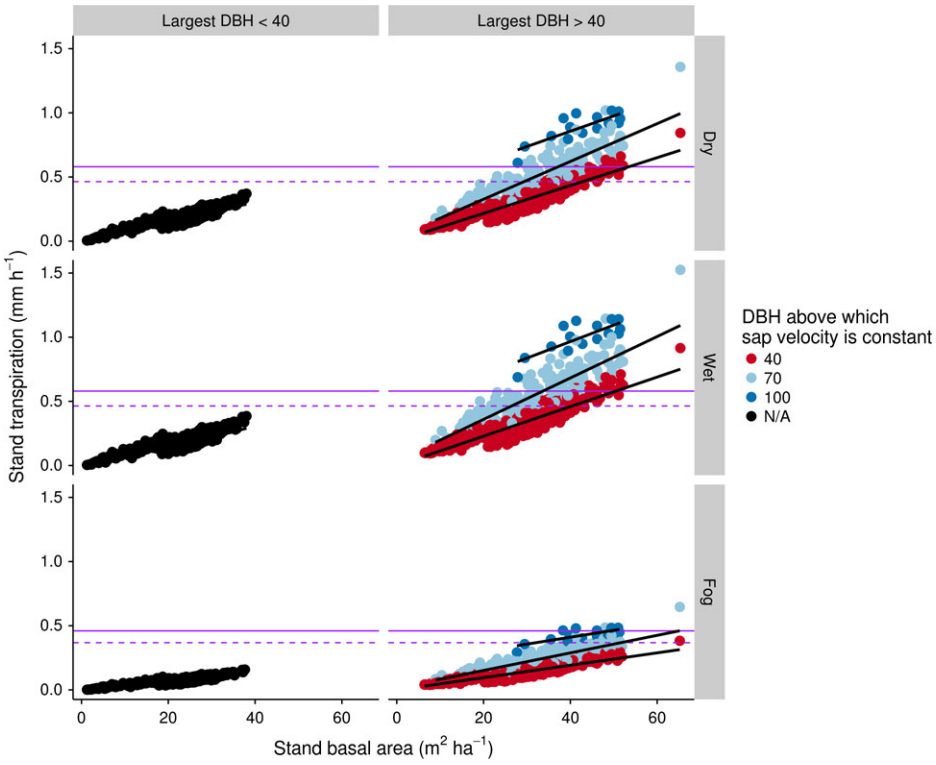

Figure 4. Modeled outputs of stand transpiration against stand basal area across dry, wet and fog seasons. Analyses were separated into plots where the largest trees were less than 40 cm DBH (left) and greater than 40 cm DBH (right). Additionally, the V_s of large trees were allowed to vary across plots, with asymptotes at 40 cm, 70 cm or 100 cm DBH to simulate a reduction in water use in large trees. Purple lines represent the corresponding net radiation and the dotted lines represent 80% of those values.

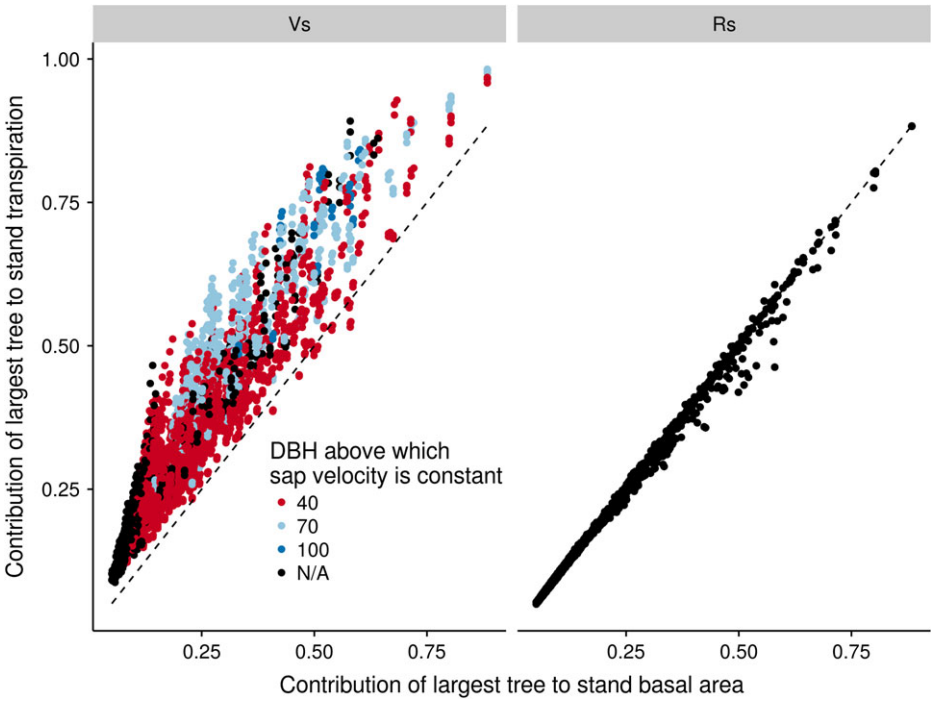

Figure 5. Modeled output of the contribution of the largest tree to stand transpiration against its contribution to stand basal area. In the left panel V_s is allowed to vary based on the point in the tree when sap velocity is held constant. The right panel holds V_s constant and allows R_s to vary as a function of the absolute sapwood depth or as a proportion of the radius.

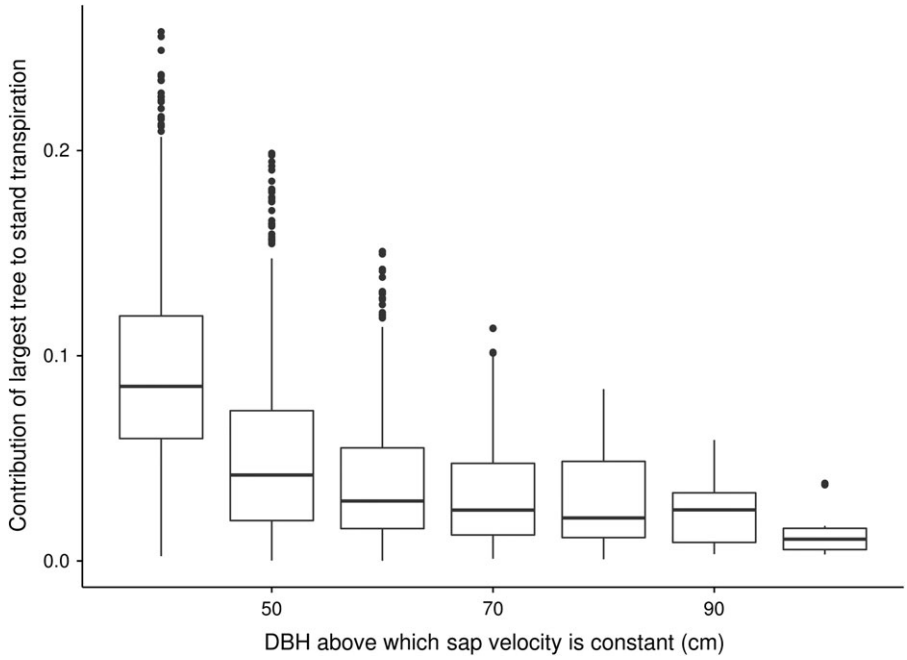

Figure 6. The difference between estimates of transpiration by the DBH at which V_s and R_s are held constant. Note that there are large differences in estimates if these values are held constant at smaller trees than larger trees. In each box plot, the midline represents the median, the box represents the first and third quartiles (25th and 75th percentiles), the whiskers represents all values within 1.5 times the interquartile range, and all individual points are values outside 1.5 times the interquartile range.

theoretical maximum was reached at progressively larger stand basal areas (Figure 4). This provides support that actual tree water use in the largest trees is likely less than expected from a linear relationship. Generally this signifies a tendency to overestimate stand transpiration for more dense plots or plots with very large trees based on current sap flow scaling methodologies.

Several prior studies have examined the relationships of sap velocity (V_s) and sapwood depth (R_s) with respect to tree size. Notably, McJannet et al. (2007) and Jung et al. (2011) found similar positive linear relationships between V_s and DBH; however, these relationships were weak. Similar linear relationships have been found between DBH and R_s (e.g., Wullschleger and King 2000, Kume et al. 2009, Jung et al. 2011, Looker et al. 2016). Although several studies have highlighted linear relationships between these parameters, this study considered alternative scaling relationships in large trees for two reasons: (i) it is likely that beyond a particular tree size there is a 'diminishing return' of water transport (Meinzer et al. 2001, 2005, Manzoni et al. 2013); and (ii) the difficulty and improbability of sampling the largest trees within the landscape necessitates extrapolation of these relationships. For example, Meinzer et al. (2005) provides strong support for asymptotic relationships in tree sap flow with diameter and aboveground biomass, particularly for angiosperms. Biologically, this is further supported by evidence that stomatal conductance strongly limits transpiration above a certain size and that tree hydraulic conductivity measurements diminish in larger trees (Mencuccini 2002, Niinemets 2002, Jaskierniak et al. 2016). Our data support the idea that there is likely a maximum value of Q at a given DBH evidenced by our comparison with the derived net radiation values. This is complementary to studies that suggest supply side constraints to water transport such as soil water capacity, resistances along the hydraulic pathway, and stomatal and boundary layer resistances at the interface with the atmosphere (e.g., Meinzer et al. 2005, Manzoni et al. 2013).

Ultimately, this manuscript provides new insights for both plant biologists and landscape hydrologists. There is a fundamental need to expand scaling practices and methodologies to address maximum water transport by the largest trees. To date, sap flow estimations of whole-tree water use in large trees typically involves sampling only the outer few centimeters of sapwood area or destructive sampling of large trees and derivation through laboratory methods (e.g., Vertessy et al. 1997). In recent literature, many excellent studies have examined radial variation in sap flow rates, which will undoubtedly improve estimates of tree and stand transpiration (Wullschleger and King 2000, Gebauer et al. 2008, Alvarado-Barrientos et al. 2013, Berdanier et al. 2016). While some studies have emphasized the importance of characterizing sapwood area (e.g., Ford et al. 2007), assessing variation in sap velocities, particularly in the largest trees, is critical for improving accuracy of E_t estimates. Further, if scaling is done with respect to sap flow parameters (V_s, R_s or P_s) instead of Q, researchers can better assess the propagated errors associated with extrapolation to unsampled trees (Oren et al. 1998). Future research should focus on integrating models of radial variation, plant hydraulics and wood anatomy to tease apart the mechanistic drivers for sap flow rates. Consequently, when scaling sap flow

measurements, researchers should consider the size distributions within plots carefully and make their best attempts to design sampling strategies to account for this potential variation and ensure adequate representation of larger trees.

In conclusion, we have utilized a rigorous combination of field and model simulations to examine how tree water use scales with size in tropical montane forests. Our modeled output takes into consideration asymptotic relationships between DBH and V_s as an alternative relationship to a constant linear increase. Using a wide range of parameters we found that stand E_t values often surpassed the net radiation at median stand basal areas, meaning that they were likely overestimated. This is driven by the large uncertainty in predicting water use in the largest trees throughout the landscape. We propose that this modeling framework is a useful tool for predicting transpiration across landscapes because it considers fundamental biological relationships and a wide range of parameters to produce consistent results of transpiration across stands with different basal areas. Additionally, based on these outputs, it is plausible that the true relationship between sap flow parameters and tree diameter is asymptotic or sigmoidal, but more detailed studies considering the tapering effect of these parameters on plant water use are urgently needed to further elucidate these scaling relationships.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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