

1    *Target journal: Ecohydrology*

2    **Title: Upscaling transpiration in diverse forests: Insights from a tropical premontane site**

3    Authors: Georgianne W Moore<sup>1\*</sup>, Graciela Orozco<sup>1,2</sup>, Luiza MT Aparecido<sup>1</sup>, Gretchen R Miller<sup>3</sup>

4

5    **Short Title: Upscaling Transpiration in Tropical Forests**

6

7    <sup>1</sup>Texas A&M University, Department of Ecosystem Science and Management, 2138 TAMU,  
8    College Station, Texas, 77843, USA.

9    <sup>2</sup>INVISTA S.à r.l., 5060 FM 1006, Orange, TX 77630, USA.

10    <sup>3</sup>Texas A&M University, Department of Civil Engineering, 3136 TAMU, College Station,  
11    Texas, 77843-3136, USA.

12

13    Co-Author E-mails (in sequence): [graciela.lydia@gmail.com](mailto:graciela.lydia@gmail.com);  
14    [luizamariabr2014@tamu.edu](mailto:luizamariabr2014@tamu.edu) ; [gmiller@civil.tamu.edu](mailto:gmiller@civil.tamu.edu)

15    \*Corresponding author: Email: [gwmoores@tamu.edu](mailto:gwmoores@tamu.edu) ; Telephone: +1(979) 845-3765.

16

17

18

19

20    **Abstract**

21    Upscaling water use of individual trees to stands using sap flux techniques is a common method  
22    for partitioning site water balance, but few such studies have occurred in the tropics. Increasing  
23    interests in the role of tropical forests in global cycles have spurred upscaling studies in natural  
24    tropical forests, which present challenges from greater tree species and functional diversity, and  
25    potential factors that would reduce transpiration, such as frequent cloud cover and wet canopy  
26    conditions. In a premontane wet tropical forest in central Costa Rica, sap flow was measured in  
27    15 trees stratified into five size classes based on tree diameters. None of the trees belonged to the  
28    same species, genus, or even family. We also accounted for potential radial variation in sap flux  
29    density. Data were scaled to estimate transpiration within a small 2.2-ha watershed using stand  
30    surveys of sapwood area. Stand transpiration averaged only  $1.4 \pm 0.7 \text{ mm d}^{-1}$  within this forested  
31    watershed due to persistent low radiation, evaporative demand, and frequent wet canopy  
32    conditions. Our systematic approach used tree size attributes to scale water use to the stand,  
33    given difficulties to quantify species differences in such a diverse ecosystem. Contrary to  
34    previous evidence on temperate trees, the large trees sampled did not exhibit flow reductions in  
35    deeper sapwood, which warrants further study. These results highlight some unique aspects of  
36    measuring transpiration in wet tropical forests that are important to consider for future studies in  
37    diverse stands.

38    **Key words:** Costa Rica; transitional rainforest; sap flux; sap flow; radial profile

39      **Introduction**

40            Evapotranspiration from tropical forests is a major source of water vapor to the  
41          atmosphere on the global scale (Fisher *et al.*, 2009) approaching 1400 mm per year (Zhang *et al.*,  
42          2010). For example, one third of precipitation that falls over the Amazon basin is supplied by  
43          recycled evapotranspiration, which is further facilitated by the deep-rooted trees (e.g., Trenberth,  
44          1999). Despite its critical role in global climate, causes of variation in tropical forest  
45          transpiration have not been closely studied. Ecohydrological processes in humid environments  
46          are fundamentally different from those in dryland regions, in that they are controlled not by acute  
47          or chronic limitations in water-availability (Porporato *et al.*, 2002), but by limitations in energy-  
48          availability (Loescher *et al.*, 2005). In these environments, plant- and canopy-centric processes,  
49          such as canopy interception, stemflow, and leaf water uptake, as well as the spatial heterogeneity  
50          in these processes, may have a profound influence on land-atmosphere fluxes (Loescher *et al.*,  
51          2002). Through these mechanisms, vegetation alters the water balance in such systems in an  
52          entirely different manner than in dryland regions (Bonan, 2008; Calder, 1998) and likely differs  
53          with land cover (Pypker *et al.*, 2005). Considering the issues with altered precipitation regimes  
54          facing tropical regions around the globe (Foster, 2001; Schuur, 2003), an improved  
55          understanding of the spatiotemporal variability in transpiration in diverse tropical forests is  
56          critically needed to predict forest responses and feedbacks to changing precipitation and species  
57          composition under future climate and land use scenarios (Fisher *et al.*, 2009).

58            Tropical montane forests (TMF) are one of the least understood and investigated  
59          ecosystems in the world, particularly in regards to hydrologic cycling (Motzer *et al.*, 2005),  
60          despite an increased interest within the last two decades to investigate the processes governing  
61          montane forests (Bruijnzeel *et al.*, 2011; Gotsch *et al.*, 2016; Oliveira *et al.*, 2014). The ratio of

62 transpiration to streamflow rates is known to be lower in TMFs than in lowland rainforests  
63 (Motzer *et al.*, 2005), perhaps because the canopies in montane areas are prone to remaining wet  
64 for longer portions of time due to cooler temperatures and increased cloud cover (Dietz *et al.*,  
65 2007).

66 The influence that leaf wetness exerts on transpiration in TMF canopies is largely  
67 unknown (Eller *et al.*, 2015; Horna *et al.*, 2011; O'Brien *et al.*, 2004). However, in a recent  
68 study, leaf wetness was shown to reduce transpiration by an additional 28%, after accounting for  
69 the effects of incident solar radiation ( $R_s$ ) and vapor pressure deficit ( $VPD$ ) (Aparecido *et al.*,  
70 2016). Energy in the form of solar radiation is a limiting variable, and evapotranspiration is  
71 closely coupled with it in lowland tropical forests across a wide range of tree species (Meinzer,  
72 2003; Meinzer *et al.*, 2003). However, our ability to accurately predict evapotranspiration in  
73 forests with frequent wet canopy conditions may require additional inputs. Thus, the frequency  
74 and intensity of rainfall could impose an important (Ishibashi and Terashima, 1995; Kume *et al.*,  
75 2011) yet poorly understood control on evapotranspiration beyond those considered by the  
76 standard models that rely only on  $R_s$  and  $VPD$  (Jones, 1992). It is possible that vertical variation  
77 in leaf wetness alters the proportioning of transpiration in the canopy. Despite clear patterns of  
78 reduced wetness duration at the top of the canopy, Aparecido *et al.* (2016) did not find large  
79 differences in the transpiration response to leaf wetness between trees in the overstory and less-  
80 exposed midstory (i.e. both proportionally decreased), which suggests plants may have  
81 developed adaptations to the frequently wet environment. By contrast, understory trees had a  
82 constant rate of water use independently of the canopy wetness condition. Nevertheless, the  
83 relative importance of canopy exposure, species adaptations to wet environments, and changes in

84 aerodynamic properties with age and stand management has not been explored extensively in  
85 these forests.

86 All tropical forests are broadly characterized by their complex structure arising from high  
87 species diversity and relative stability of annual and interannual climate cycles. For tropical  
88 rainforest trees, researchers (e.g., Wright *et al.*, 2005) have hypothesized that species-specific  
89 differences in physiology, morphology, and architecture, as well as environmental influences,  
90 including site microclimate and topography, contribute to variation in functional traits that  
91 determines species occurrence and coexistence. While it is well known that climate gradients in  
92 montane environments amplify the spatial variability in species composition along ecotonal  
93 boundaries, the effect of species-specific differences on transpiration is less clearly understood.  
94 The few studies that address this in Neotropical forests have suggested that variation in  
95 transpiration is controlled less by species-specific differences than by physical tree attributes,  
96 including tree height and hydraulic architecture (Andrade *et al.*, 1998; Kunert *et al.*, 2017;  
97 Meinzer *et al.*, 2001). Given many upscaling studies in temperate forests apportion transpiration  
98 within stands using species-specific sap flux estimates (Ewers *et al.*, 2002; Granier and Lostau,  
99 1994; Moore *et al.*, 2004; Oren *et al.*, 1999), such approaches may be inappropriate in diverse  
100 tropical forests.

101 We investigated transpiration at the tree-to-stand scale in a tropical premontane forest in  
102 Costa Rica. The objectives of this study were to determine: (1) how transpiration responds to  
103 primary drivers, specifically solar radiation and atmospheric vapor pressure deficit, and whether  
104 those responses differ with tree characteristics; and (2) how rainfall and canopy wetness affects  
105 temporal patterns in transpiration. This work also will be directly compared with the results  
106 presented by Aparecido *et al.* (2016) in a nearby location ~250-m southeast, who estimated 497

107 mm annual transpiration in a study of 17 species from which only 3 species overlap with this  
108 study.

109 The following assumptions underlie this study: (1) Tropical montane tree species can be  
110 reasonably classified into functional groups according to size in order to predict transpiration. As  
111 such, failure to represent a wide range of tree sizes in sap flux studies is likely to bias estimates  
112 of stand transpiration; and (2) All species are similar in their water use, after accounting for  
113 differences related to canopy position and tree size.

114

## 115 **Materials and Methods**

### 116 *Study Area*

117 The study was conducted at the Texas A&M University Soltis Center for Research and  
118 Education near San Isidro de Peñas Blancas, Costa Rica ( $10^{\circ} 23.0' N$ ,  $84^{\circ} 37.0' W$ ). The Soltis  
119 Center is comprised of 250-ha of mixed secondary and primary forest, ranging from 450 to 650  
120 masl and adjacent to the Children's Eternal Rainforest preserve. The vegetation is a transitional  
121 tropical premontane moist forest situated at higher elevations than surrounding lowland forests,  
122 but below that of cloud affected forests of the Monteverde highlands (Holdridge, 1967). Trees  
123 range from 25-35 m in height, reaching upper canopy at around 25 m with dense foliage,  
124 multiple interlacing crowns, but with frequent canopy gaps. The geology consists of volcanic  
125 mudflows and landslides, with underlying saprolitic tuff. The soil is andisolic with clay to clay-  
126 loam texture, and originates from Caribbean volcanic ash.

127 Weather variables have been continuously monitored at the Soltis Center since June 2010  
128 using a combination of manual rain gauges and an on-site meteorological tower. Annual rainfall  
129 is approximately 5000 mm, with a rainy season from May to December and a relatively “dry”  
130 season from January to April when monthly rainfall totals are ~60% less than in rainy season.  
131 Air temperature shows little seasonal variation, with monthly averages ranging from 21 to 24°C,  
132 a low of 15°C, and a high reaching 32°C (Fig. 1). Solar radiation ( $R_s$ , W m<sup>-2</sup>) is highest during  
133 the dry season. A small, 2.2-ha watershed, known locally as “Howler Hollows”, has been the  
134 subject of previous investigations (e.g., Buckwalter *et al.*, 2012; DuMont *et al.*, 2013; Houser *et*  
135 *al.*, 2013; Teale *et al.*, 2014; Washington-Allen *et al.*, 2012), and defines the spatial extent of this  
136 study site.

137

### 138 *Stand Characterization*

139 Four 30-m diameter plots were randomly delineated within the watershed. Diameters  
140 (DBH) of all 92 trees within the plots were measured (Fig. 2a). To determine active-xylem  
141 sapwood depth, we visually inspected 5-mm cores with the aid of safranin dye as described in  
142 Aparecido *et al.* (2016). Xylem depth was assessed on each tree equipped with sap flow sensors  
143 and an additional 26 trees spanning the full range in diameters. From these measurements, a  
144 basal area to sapwood area relationship was developed to estimate sapwood area of the  
145 unmeasured trees (Fig. 2b) and a histogram of the percentage of total sapwood area by tree  
146 diameter (Fig. 2c).

147 One of the four plots was selected for the placement of sap flow sensors based on  
148 proximity to a nearby clearing where solar panels were located. The other plots were not

149 accessible for sap flux measurements. Typically, sap flux studies measure only the dominant tree  
150 species, four species at most, and replicate by species at a given site to determine each species'  
151 contribution to stand transpiration (Moore *et al.*, 2004; Wullschleger *et al.*, 2001). However, our  
152 ability to compare variation within species was limited due to the high diversity within the plot,  
153 as few species had more than one tree represented. Instead, following our assumption that tree  
154 size was a controlling factor for sap flux rates, we randomly selected three trees within each of  
155 five diameter ranges to receive sensors (Table 1). Having five size categories helped evenly  
156 distribute tree selection across the full range of tree diameters in the plot (i.e., distribution, rather  
157 than replication, was the systematic approach utilized). Each of the 15 trees was a unique species  
158 originating from 15 unique families (Table 2).

159

160 *Transpiration Measurement and Upscaling*

161 Transpiration rates were determined for the 15 trees using heat dissipation sap flow  
162 sensors (Granier, 1985) that were laboratory made using the methods described in Phillips *et al.*  
163 (1997). Each tree had two sensors installed on opposite sides, perpendicular to the slope, at ~1.4  
164 m measuring sap velocity in the outer 20 mm of xylem. Measurements were taken every 30 s and  
165 averaged within trees every 10 min from January 16 to November 14, 2012 (total of 10 months).  
166 Sap flux density ( $J_s$ , kg m<sup>-2</sup> s<sup>-1</sup>) was calculated based on the following equation:

167 (2) 
$$J_s = 0.119 \cdot K^{1.231}$$

168 where  $K$  is a dimensionless constant determined by the following equation:

169 (3) 
$$K = (\Delta T_M - \Delta T) / \Delta T$$

170  $\Delta T_M$  is the maximum temperature difference when sap flux is assumed to be zero, and  $\Delta T$  is the  
171 actual temperature difference between the two probes, calculated from the mV output. Due to the  
172 high frequency of  $VPD = 0$  at our site, zero flows were determined on a daily basis.

173 Previous papers have called attention to the need to determine the radial sapwood profile  
174 of the velocities in order to upscale from sap velocity to the total volumetric sap flow of a tree  
175 (Caylor and Dragoni, 2009; Dragoni *et al.*, 2009). To determine if this correction was necessary  
176 in this study, depth profile measurements of sap flux density (Fig. 3) were obtained in six of the  
177 larger trees using compensation heat pulse profile probes inserted to a depth of 60 mm with  
178 measurements every 10 mm (Green *et al.*, 2003) over a period of several days. However, the  
179 profiles deviated significantly from the previously published model for angiosperms in temperate  
180 areas (Ford *et al.*, 2007; Pataki *et al.*, 2011). These previous models were based on a Gaussian  
181 curve, given as:

182 (4) 
$$J_i/J_o = a \cdot \exp \left[ -0.5 \left( \frac{x-b}{c} \right)^2 \right]$$

183 where  $J_i/J_o$  is the relative flux,  $x$  is the relative sapwood depth, and  $a$ ,  $b$ , and  $c$  are fitted  
184 parameters. We tested three potential models against our data (Fig. 3): a Gaussian curve using  
185 the parameters reported by Pataki *et al.* (2011) ( $a = 1.033$ ,  $b = 0.0996$ ,  $c = 0.4263$ ), a Gaussian  
186 curve with best-fit parameters ( $a = 1.034$ ,  $b = 0$ ,  $c = 1.440$ ), and a linear regression model ( $m = -$   
187  $0.24$ ,  $y_0 = 1.77$ ). The Nash-Sutcliffe efficiency coefficient (NSE) was calculated for each to  
188 compare its predictive power against a null (no slope) model. The Gaussian model with Pataki  
189 parameters had an  $NSE = -5.2$ , indicating that the mean of the data was a far better predictor than  
190 the model itself. The best-fit Gaussian curve ( $NSE = 0.19$ ,  $p < 0.01$ ) and the linear model ( $NSE =$

191 0.22, p<0.001) gave better predictions. Additionally, size-related differences in profile patterns  
192 were not detected, nor were patterns consistent between trees.

193 Given the profiles measured and their high degree of variation, we chose to assume a  
194 constant sap flux density throughout the sapwood area. Total transpiration per tree ( $Q$ ) was found  
195 using the equation:

196 (5)  $Q_i = \bar{J}_{s,l} A_i \rho_s$

197 where  $Q_i$  is an individual tree  $i$ 's total volumetric sap flow rate ( $\text{m}^3 \text{ s}^{-1}$ ),  $\bar{J}_{s,l}$  is mean sap flux  
198 density (Eq. 2),  $A_i$  is the tree's total sapwood area (Table 1,  $\text{m}^2$ ), and  $\rho_s$  is the density of its sap,  
199 equal to that of water,  $1.0 \text{ g cm}^{-3}$ . Total tree water use was reported in units of  $\text{L d}^{-1}$ .

200 Similarly, to estimate stand transpiration at the watershed scale, the following equation  
201 was used:

202 (6)  $Q_T = \sum_{k=1}^5 \bar{J}_{s,k} A_k \rho_s$

203 where  $Q_T$  is the volumetric flow of water from all trees in the watershed ( $\text{m}^3 \text{ s}^{-1}$ ),  $\bar{J}_{s,k}$  is the mean  
204 sap flux density from the three instrumented trees in size class  $k$ , and  $A_k$  is the total sapwood area  
205 for all trees in size class  $k$  (Table 2). To find the mean estimated transpiration rate over the  
206 watershed,  $T$  ( $\text{mm}$ ),  $Q_T$  is divided by the total watershed area,  $A_w$ , equal to  $22,000 \text{ m}^2$  for this  
207 study:

208 (7)  $T = Q_T / A_w$

209 *Climate Measurements*

210            Climatic variables were measured on a nearby 10-m micrometeorological tower located  
211        in a small clearing instrumented with a pyranometer (LI-200, LI-COR, Lincoln, Nebr.), tipping  
212        bucket rain gauge (TE525WS, Campbell Scientific Inc., Logan, UT), and temperature and  
213        relative humidity sensor (HMP45C, Campbell Scientific) from which vapor pressure deficit  
214        (*VPD*) was calculated. Leaf wetness was estimated using two LWS sensors at 1.5 m above the  
215        ground surface (Decagon Devices, Pullman, Wash.): one at a nearby location below the canopy  
216        and the other in a nearby open area. All measurements were compiled at 5-minute intervals.  
217        LWS data were only available for limited periods in the wet season of 2011 and 2012. The use of  
218        dielectric sensors as a proxy for actual leaf wetness is limited by several factors, including leaf  
219        surface traits to retain or repel water (Armstrong *et al.*, 1993; Sentelhas *et al.*, 2004) and the high  
220        level of spatial variation in wetness condition and duration throughout a complex canopy  
221        (Giesler *et al.*, 1996; Magarey *et al.*, 2005). Therefore, we constrain our use of LWS data to  
222        generalized relationships between sap flux and leaf wetness.

223        *Data analyses*

224        Linear and non-linear model fits were applied to determine the degree of relationship  
225        between daily total transpiration (dependent variable) and daily average climatic variables (*VPD*,  
226         $R_s$ ) during daylight hours (independent variables). Best model fit was determined by the  
227        coefficient of variation ( $r^2$ ), Pearson correlation ( $r$ ) and p-values ( $\alpha < 0.01$ ). The analysis was  
228        done in the R-software package (version 2.13.1) (R Core Team, 2013). The general linear model  
229        function [lm()] was used to fit a linear model to climatic variables in log-transformed and non-  
230        transformed forms, and the non-linear model function [nls] was used to fit an exponential power  
231        model. Regression models were also used to test for relationships between average sap flux  
232        density per tree and total tree water use with tree diameter, as indicated by  $r^2$  and  $\alpha < 0.05$ .

233

234 **Results**

235 *Environmental Controls on Sap Flux*

236 Day 178 represents a typical, but rare, rain free day (Fig. 4 “Dry Day”). From Aparecido  
237 *et al.* (2016), only 27% of days that year had wet leaves less than 10% of the daylight hours. On  
238 dry days, such as day 178, sap flux rates tracked solar radiation ( $R_s$ ), with VPD having a  
239 secondary influence. Day 181 represents a day with significant leaf wetness that influenced  $J_s$   
240 after the rain ended (Fig. 4 “Wet Day”). After sunrise on the wet day, radiative and evaporative  
241 demands increased dramatically while  $J_s$  remained near zero until leaves were sufficiently dry.  
242 On wet mornings, such as day 181,  $J_s$  lagged behind  $R_s$  for about 2 hours, until the leaves dried  
243 out below 80% leaf wetness. Such a lag could also be associated with stem water storage;  
244 however, lags were longer on wet mornings than dry mornings. This suggests a threshold for leaf  
245 wetness of approximately 80% above which transpiration does not occur. While  $J_s$  ceases during  
246 periods of saturated leaf wetness (LW>80%), evaporation of intercepted rainfall continues, given  
247  $VPD > 0$  kPa at the wet leaf surface.

248 Over long time periods containing a mix of wet and dry days,  $J_s$  among trees in size class  
249 5 was more closely related to  $R_s$  than VPD ( $r^2 = 0.52$  and 0.32, respectively,  $p < 0.01$ , Fig. 5a  
250 and 5b). Sap flux rates were highly variable at higher levels of VPD (above 1 kPa), but tended to  
251 approach a maximum at high levels of VPD (Fig. 5a), which was much lower in trees of class 1–  
252 4 than class 5. Similarly,  $J_s$  was more variable at higher levels of  $R_s$ , particularly in class 5 trees,  
253 but did not indicate any suppression of  $J_s$  at high  $R_s$  (Fig. 5b). During the wet season,  $J_s$  peaked  
254 in the early afternoon with all classes having similar patterns throughout the day (Fig. 6a). Size

255 classes 4 and 1 had the highest  $J_s$  rates, while class 2, 3 and 5 were the lowest (Fig. 6a). Most of  
256 these trends continued into the dry season, but maximum  $J_s$  was higher and occurred earlier,  
257 around midday (Fig. 6b). When sap flux densities were grouped by time of day (morning versus  
258 afternoon), distinct differences in these relationships were noted, indicating the presence of  
259 hysteretic behavior (Fig. 7), indicating that the response to  $VPD$  and  $R_s$  was time-dependent. In  
260 general, when given the same  $VPD$ , sap flux rates were higher in the mornings than the  
261 afternoons (Figs. 7c,e). However, on dry days only, this trend reversed for late afternoon and  
262 early evening values. These patterns were similar among all size classes, but class 5 had  
263 consistently higher sap flux than classes 1–4 on wet mornings; whereas, on dry days, differences  
264 in diurnal trends between size classes were less notable (Fig. 7c,e). While the average diurnal  
265 trends in  $R_s$  were similar on wet and dry days (Fig. 7b), substantial differences were noted in the  
266 areas of their hysteresis loops for both size groupings (Figs. 7d,f), indicating greater contrasts  
267 between morning and afternoon responses. On wet days, sap flux density had similar morning  
268 and afternoon behaviors; similar light levels had only small differences. However, on dry days,  
269 rates were much higher in the afternoons than in the mornings, given the same level of light.

270 Individual tree estimates of mean  $J_s$  were not related to tree diameter (Fig. 8a,  $p > 0.05$ ),  
271 but tree diameter was a good predictor of total tree water use ( $r^2 = 0.89$ , Fig. 8b). The large  
272 *Carapa* tree, being nearly 3× larger than the next-largest tree, exerted high leverage on the  
273 regression fit.

274

275 *Stand Level Transpiration*

276 Over a 10-month period in 2012, stand transpiration approached a maximum rate of 3.0  
277 mm d<sup>-1</sup>, but was often much lower (Fig. 9), averaging  $1.4 \pm 0.7$  mm d<sup>-1</sup>. A disproportionate  
278 fraction of total stand transpiration came from the largest diameter trees, class 5, which  
279 contributed more than 80% to the stand total. This was attributed to a greater total sapwood area  
280 in class 5, rather than higher sap flux density (Fig. 9, Table 1).

281

## 282 Discussion

### 283 *Insights in upscaling transpiration in tropical forests*

284 Our study addresses a critical theme in the field of ecohydrology that seeks to better  
285 understand the contrasts between water-limited and energy-limited systems and to apply those  
286 principles across scales (Asbjornsen *et al.*, 2011). Furthermore, it contributes to the growing  
287 body of work to optimize sap flux scaling methods from trees to stands (Čermák *et al.*, 2004;  
288 Kostner, 2001; Oren *et al.*, 1998) to watersheds (Ford *et al.*, 2007; Moore *et al.*, 2004) by  
289 extending these concepts to diverse tropical forests. In our study, stand transpiration amounted to  
290 only  $1.4 \pm 0.7$  mm d<sup>-1</sup> due to persistent low radiation, evaporative demand, and frequent wet  
291 canopy conditions. These results matched transpiration estimates of Aparecido *et al.* (2016)  
292 nearby site, which were  $1.4 \pm 0.5$  mm d<sup>-1</sup> over a 12-month period in 2014.

293 Given the challenges of quantifying species differences in such a diverse ecosystem, our  
294 findings suggest that tree size can serve as an appropriate scalar for water use in tropical forests  
295 where estimates of species-level mean values are impractical. This arises where species  
296 replicates are spaced very far apart or where transpiration is widely distributed among  
297 individuals of many species, each contributing only a small fraction to site water balance. Our

298 stand consisted of more than 15 unique families, with only minor overlap between the genus or  
299 species at the study site only 250-m away (Aparecido *et al.*, 2016). Those in common between  
300 the two sites were *Inga* sp. (n=1), *Brosimum* sp. (n=1) and *Carapa guianensis* (n=3), which were  
301 categorized as Class 5, Class 3, and Classes 5, 3 and 2, respectively. It was apparent that any  
302 inherent trait unique to a particular genus or species was extremely difficult to distinguish from  
303 other size and edaphic factors; for instance, even those within the same diameter class had  
304 differing canopy exposure.

305 For instance, on average, sap flux density of *Inga* sp. ( $521 \text{ kg m}^{-2} \text{ d}^{-1}$ , 40-cm diam.),  
306 reported by Aparecido *et al.* (2016), was only 1/3 the rates observed in the *Inga* sp. in this study  
307 ( $1552 \text{ kg m}^{-2} \text{ d}^{-1}$ , 28-cm diam.) despite its larger size. To the contrary, sap flux density of  
308 *Brosimum* sp. ( $308 \text{ kg m}^{-2} \text{ d}^{-1}$ , 19-cm diam.), also reported by Aparecido *et al.* (2016), was 50%  
309 greater than the rates observed in the *Brosimum* sp. in this study ( $197 \text{ kg m}^{-2} \text{ d}^{-1}$ , 42-cm diam.).  
310 Interestingly, the *Carapa guianensis* individual in this study with such a large diameter (120 cm)  
311 had very similar rates of sap flux as a 43-cm diameter individual reported by Aparecido *et al.*  
312 (2016), 628 and  $647 \text{ kg m}^{-2} \text{ d}^{-1}$ , respectively. The other two *Carapa guianensis* individuals from  
313 Aparecido *et al.* (2016) had lower rates of 209 and  $134 \text{ kg m}^{-2} \text{ d}^{-1}$  and diameters of 17 and 8 cm,  
314 respectively. This provides only limited support for our assumption that tree size may be a better  
315 way to partition transpiration within a stand than species, since size appeared to affect  
316 differences among *Inga* and *Carapa* individuals, but not *Brosimum*. Such a mismatch is  
317 reasonable, given that crown exposure is a likely factor influencing rates of  $J_s$  within species,  
318 whereas, total tree water use is more a function of cross-sectional conducting xylem. We used  
319 basal diameter rather than crown size or exposure to classify trees for this study. It is clear from  
320 Table 2 that height and diameter were weakly correlated. Height was an equally poor predictor of

321  $J_s$  as diameter was (Fig. 8, height results not shown, see Table 2). Yet, tree diameter explained  
322 nearly 90% of the variation in total tree water use (Fig. 8), largely as a function of sapwood area;  
323 although the large *Carapa* tree had a lower sapwood area for its size than the smaller trees (Fig.  
324 2b). One species, *Inga* sp., had much higher than predicted water use for its size, while another  
325 species, *Brosimum* sp., had much lower than predicted water use for its size. Although we were  
326 unable to resolve any species-related trends, our systematic approach to sample across tree  
327 diameters resulted in a robust stand transpiration estimate. Nevertheless, a study with higher  
328 replication within species is required to elucidate the relative contribution to stand transpiration  
329 among co-occurring species.

330 Our study site consisted of a smaller size cohort of secondary regrowth trees than the  
331 stand studied by Aparecido *et al.* (2016), and our small trees contributed more to the total  
332 sapwood area of the stand. This suggests that the relative proportion of water use by size  
333 category cannot be generalized across sites. Being able to make generalities about water use  
334 patterns is particularly important in highly diverse stands where species-level estimates are not  
335 feasible. We recommend our systematic sampling approach to characterize water use for a  
336 representative array of tree sizes, rather than a representative array of tree species, in sites with  
337 high diversity.

338 A comparison between the large exposed trees in size class 5 and the other smaller trees  
339 in class 1–4 indicated some interesting temporal patterns on a subdaily basis that differ between  
340 wet and dry conditions (Fig. 7). In water-limited environments, greater magnitudes of hysteresis  
341 (area within the loop) for VPD have been associated with overnight rehydration (higher morning  
342  $J_s$ ) and stomatal limitation (lower afternoon  $J_s$ )—especially in the drier months, associated with  
343 lower soil water potential (Zhang *et al.*, 2014; Zheng *et al.*, 2014). However, no previous study

344 has implicated leaf wetness as a driver of hysteretic trends (Zhang *et al.*, 2014), which may be  
345 influenced by plant adaptations to wet leaf conditions in the humid topics (Aparecido *et al.*,  
346 2017). We observed a larger magnitude of hysteresis for  $R_s$  on dry days compared to wet days  
347 than previously reported (Zheng *et al.*, 2014). On ‘dry’ mornings, the lagged sap flux response to  
348  $R_s$  (Fig. 7d) is likely due to wet leaves from overnight rain or dew. Consequently, it is reasonable  
349 to expect a much higher proportion of site water balance allocated from evaporation to  
350 transpiration once the canopy dried. This effect diminishes on wet days, as wetness often persists  
351 into the afternoon because of periodic rain showers. Observed differences between size classes  
352 further substantiate this, since class 1–4 hysteresis patterns contrasted more between wet and dry  
353 days than the more exposed (presumably faster drying) trees in class 5. The upper canopy of tall  
354 forests such as this is aerodynamically rough and more coupled to the atmosphere than the lower  
355 canopy layers where air is less mixed (Jones, 1992). Quantitative assessments of leaf wetness  
356 variation and its effects throughout the canopy are needed, since our leaf wetness data could not  
357 be used to make direct comparisons of wetness condition between size classes.

358 When extrapolating the average daily transpiration of  $1.4 \text{ mm d}^{-1}$  over the 10 month  
359 measurement period to a full year, annual transpiration is approximately  $511 \text{ mm yr}^{-1}$ , which is  
360 consistent with other findings in literature for similar vegetation types, especially in tropical  
361 montane cloud forests that are known to have transpiration around  $250\text{--}645 \text{ mm year}^{-1}$   
362 (Bruijnzeel and Veneklaas, 1998). Estimates from tropical montane cloud forests were between  
363  $355$  and  $645 \text{ mm year}^{-1}$ , depending on elevation, with lower values at highest elevations  
364 (Bruijnzeel *et al.*, 2011; McJannet *et al.*, 2007). Within lowland tropical forests, Horna *et al.*  
365 (2011) reported daily transpiration rates from  $0.09$  to  $1.05 \text{ mm day}^{-1}$  and an annual total of only  
366  $253 \text{ mm}$  for a mature tropical Indonesian stand; Kunert *et al.* (2015) found annual total stand

367 transpiration of 845 mm year<sup>-1</sup>, and ranging from 0.29 to 4.74 mm day<sup>-1</sup> in a mature Amazonian  
368 forest stand; and in a pine plantation in Mexico, Alvarado-Barrientos *et al.* (2014) found that  
369 transpiration was greater during sunny conditions with  $2.6 \pm 0.2$  mm day<sup>-1</sup>, and lowest during fog  
370 events with  $0.3 \pm 0.1$  mm day<sup>-1</sup>, with an annual total of ~650 mm.

371       Others have scaled transpiration to the stand using similar methods as ours (Bucci *et al.*,  
372 2008; Granier *et al.*, 1996; Horna *et al.*, 2011), for example, by using a range of tree diameters  
373 (Horna *et al.*, 2011) or a range of crown dominance (Aparecido *et al.*, 2016; Kunert *et al.*, 2017).  
374 More commonly, though, measurements extend only to individual trees (Kunert *et al.*, 2015;  
375 Meinzer *et al.*, 2004; O'Brien *et al.*, 2004). However, we caution against subsampling biases that  
376 tend to overestimate stand transpiration if, for example, instrumented trees are predominantly in  
377 the larger class sizes (i.e., overstory). Aparecido *et al.* (2016) clearly identified  
378 disproportionately lower transpiration in understory trees. Considering that leaves dry out more  
379 slowly in the lower canopy, tropical understory trees may use proportionately less water than  
380 temperate understory trees, relative to the overstory. Horna *et al.* (2011) also pointed out the  
381 importance of accurate representation of understory trees and accounted for it in Indonesian  
382 forests. More accurate estimates of transpiration are needed to better partition biological  
383 responses to changing water resources across the globe (Jasechko *et al.*, 2013).

384       While  $R_s$  and  $VPD$  were strong drivers of transpiration responses, we also found evidence  
385 that leaf wetness suppressed transpiration until a significant threshold of dryness was surpassed.  
386 This is important given how frequently leaves were wet in this system, and also suggests that  
387 transpiration may be suppressed by leaf wetness in other humid regions (Alvarado-Barrientos *et*  
388 *al.*, 2014; Berry *et al.*, 2016; Chu *et al.*, 2014; Gotsch *et al.*, 2014; Reinhardt and Smith, 2008;  
389 Ritter *et al.*, 2008). We observed that transpiration during the two driest months with full

records (February and March) was about 26% lower than the two wettest months (July and September, see Figure 10). However, observations in the Amazon rainforest indicated that plants responded more strongly to soil moisture fluctuations (Malhi *et al.*, 2002). Empirical evidence of stomatal behavior under short-term high VPD or short-term declines in soil moisture is inconsistent for lowland tropical forests (Roberts *et al.*, 2005) and even rarer for montane tropical rainforests. Ultimately, the interplay between atmospheric demand, leaf wetness, and soil water limitation determines whether transpiration increases or decreases, depending on the relative strength of these opposing responses.

We found only modest decreases in transpiration during drier months (Figure 7), when transpiration is expected to account for a greater portion of the water budget. Compared with the extensive studies of transpiration responses to water deficits in temperate regions, considerably less is known about the onset of drought-related reductions in transpiration in the wet tropics, with potential implications for water resources management and early detection of drought stress. Likewise, our largest trees show no evidence of suppressed water use when dry. Our study showed that, by far, the largest trees make up the greatest contribution of total sapwood in this stand. This is important for several reasons. First, large trees in temperate regions tend to have lower proportions of sapwood area to total basal area than those in tropical regions, which suggests large old-growth tropical trees are growing more actively than their temperate counterparts; see Moore *et al.* (2004) for a case where temperate old-growth trees are relatively lower water users. Second, large tropical tree canopies are more exposed and thus dry out more rapidly than the understory. Third, selective harvest of a few large trees can be expected to disproportionately reduce stand sapwood area, at least temporarily, which could alter site water

412 balance (Breda *et al.*, 1995) – By contrast, see Moore *et al.* (2012), Ilstedt *et al.* (2016) and Lane  
413 *et al.* (2001) for cases where thinning forests only temporarily altered water balance, if at all.

414

## 415 **Conclusions**

416 This study characterized variable responses to environmental drivers of transpiration,  
417 which were more pronounced in larger trees. Wet leaf conditions apparently affected  
418 transpiration of smaller sized trees the most, since the lower canopy leaves remained wet for  
419 longer durations (Aparecido *et al.*, 2016). Based on these findings, we recommend an approach  
420 to scaling transpiration that neither overestimates water use of small understory trees, nor  
421 underestimates water use of dominant exposed trees. Hence, in tropical premontane forests, a  
422 more accurate estimation of stand transpiration should reasonably account for tree size variability  
423 and canopy exposure over a range of climatic conditions, including wet leaves. Applying these  
424 insights for upscaling sap flow measurements to tropical stands and watersheds are necessary to  
425 improve global and regional climate modelling, forest management practices, and policy-making  
426 strategies for a more sustainable environment.

427

## 428 **Acknowledgements**

429 We would like to acknowledge the following for their contributions to the field work  
430 associated with this project: Kevin Davis, Tomasz Fallkowski, Bryan Tarbox, and Robert  
431 Washington-Allen for stand characterization; Kelly Brumbelow, Tony Cahill, Ester Buckwalter,  
432 Andrea DuMont and Nathan Tourtellotte for streamflow measurement; Steven Quiring and

433 Oliver Fraudentfeld for weather data; Chris Houser for watershed mapping; and Eugenio  
434 Gonzalez and the Soltis Center staff for logistics. Funding was provided through the NSF grant  
435 EAR-1004874 ‘REU Site: Eco-Hydrology of a Tropical Montane Cloud Forest,’ by the U.S.  
436 Department of Energy, Office of Science, Biological and Environmental Research (DE-  
437 SC0010654), and by the Soltis and Hammer families.

438

439

440 **Literature Cited**

- 441 Alvarado-Barrientos MS, Holwerda F, Asbjornsen H, Dawson TE, Bruijnzeel LA. 2014. Suppression of  
442 transpiration due to cloud immersion in a seasonally dry Mexican weeping pine plantation.  
443 *Agricultural and Forest Meteorology* **186**: 12-25.
- 444 Andrade JL, Meinzer FC, Goldstein G, Holbrook NM, Cavelier J, Jackson P, Silvera K. 1998. Regulation of  
445 water flux through trunks, branches, and leaves in trees of a lowland tropical forest. *Oecologia*  
446 **115**: 463-471. DOI 10.1007/s004420050542.
- 447 Aparecido LMT, Miller GR, Cahill AT, Moore GW. 2016. Comparison of tree transpiration under wet and  
448 dry canopy conditions in a Costa Rican premontane tropical forest. *Hydrological Processes* **30**:  
449 5000-5011. doi: 10.1002/hyp.10960.
- 450 Aparecido LMT, Miller GR, Cahill AT, Moore GW. 2017. Leaf surface traits and water storage retention  
451 affect photosynthetic responses to leaf surface wetness among wet tropical forest and semiarid  
452 savanna plants. *Tree Physiology In Press*: 10.1093/treephys/tpx092.
- 453 Armstrong R, Barthakur NN, Norris E. 1993. A comparative study of three leaf wetness sensors.  
454 *International Journal of Biometeorology* **37**: 7-10.
- 455 Asbjornsen H, Goldsmith GR, Alvarado-Barrientos MS, Rebel K, van Osch FP, Rietkerk M, Chen J, Gotsch  
456 SG, Tobon C, Geissert DR, Gómez-Tagle A, Vache K, Dawson TE. 2011. Ecohydrological advances  
457 and applications in plant-water relations research: a review. *Journal of Plant Ecology* **4**: 3-22.
- 458 Berry ZC, Gotsch SG, Holwerda F, Munoz-Villers LE, Asbjornsen H. 2016. Slope position influences  
459 vegetation-atmosphere interactions in a tropical montane cloud forest. *Agricultural and Forest  
460 Meteorology* **221**: 207-218.
- 461 Bonan GB. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests.  
462 *Science* **320**: 1444-1449. 10.1126/science.1155121.
- 463 Breda N, Granier A, Aussenac G. 1995. Effects of thinning on soil and tree water relations, transpiration  
464 and growth in an oak forest (*Quercus petraea* (Matt.)Liebl.). *Tree Physiology* **15**: 295-306.
- 465 Bruijnzeel LA, Mulligan M, Scatena FN. 2011. Hydrometeorology of tropical montane cloud forests:  
466 emerging patterns. *Hydrological Processes* **25**: 465-498. 10.1002/hyp.7974.
- 467 Bruijnzeel LA, Veneklaas EJ. 1998. Climatic conditions and tropical montane forest productivity: the fog  
468 has not lifted yet. *Ecology* **79**: 3-9.
- 469 Bucci SJ, Scholz FG, Goldstein G, Hoffman WA, Meinzer FC, Franco AC, Miralles-Wilhelm F. 2008.  
470 Controls on stand transpiration and soil water utilization along a tree density gradient in a  
471 Neotropical savanna. *Agricultural and Forest Meteorology* **148**: 839-849. doi:  
472 10.1016/j.agrformet.2007.11.013.
- 473 Buckwalter E, Tourtellotte N, Brumbelow K, Cahill T, Miller GR. 2012. Hydrological Processes in a Pre-  
474 montane Tropical Forest. In: AGU Fall Meeting, San Francisco, California
- 475 Calder IR. 1998. Water use by forests, limits and controls. *Tree Physiol* **18**: 625-631.
- 476 Caylor KK, Dragoni D. 2009. Decoupling structural and environmental determinants of sap velocity: Part  
477 I. Methodological development. *Agr. Forest Meteorol.* **149**: 559-569.
- 478 Čermák J, Kučera J, Nadezhina N. 2004. Sap flow measurements with some thermodynamic methods,  
479 flow integration within trees and scaling up from sample trees to entire forest stands. *Trees* **18**:  
480 529-546. 10.1007/s00468-004-0339-6.
- 481 Chu H, Chang S, Klemm O, Lai C, Lin Y, Wu C, Lin J, Jiang J, Chen JM, Gotthens JF, Hsia Y. 2014. Does  
482 canopy wetness matter? Evapotranspiration from a subtropical montane cloud forest in Taiwan.  
483 *Hydrological Processes* **28**: 1190-1214.
- 484 Dietz J, Leuschner C, Holscher D, Kreilein H. 2007. Vertical patterns and duration of surface wetness in  
485 an old-growth tropical montane forest, Indonesia. *Flora* **202**: 111-117.

- 486 Dragoni D, Caylor KK, Schmid HP. 2009. Decoupling structural and environmental determinants of sap  
487 velocity: Part II. Observational application. *Agr. Forest Meteorol.* **149**: 570-581.
- 488 DuMont A, Miller GR, Cahill T, Brumbelow K, Moore G, Roark B, Buckwalter E. 2013. Water Budget of a  
489 Tropical Montane Forest, with Insights from Stable Isotope Analysis. In: Annual ATBC-OTS Joint  
490 Meeting, San Jose, Costa Rica
- 491 Eller CB, Burgess SSO, Oliveira RS. 2015. Environmental controls in the water use patterns of a tropical  
492 cloud forest tree species, *Drimys brasiliensis* (Winteraceae). *Tree Physiology* **35**: 387-399.
- 493 Ewers BE, Mackay DS, Gower ST, Ahl DE, Burrows SN, Samanta SS. 2002. Tree species effects on stand  
494 transpiration in northern Wisconsin. *Water Resources Research* **38**: 8-1-8-11.
- 495 Fisher JB, Malhi Y, Bonal D, Da Rocha HR, De Araujo AC, Gamo M, Goulden ML, Hirano T, Huete AR,  
496 Kondo H, Kumagai T, Loescher HW, Miller S, Nobre AD, Nouvellon Y, Oberbauer SF, Panuthai S,  
497 Rouspard O, Saleska S, Tanaka K, Tanaka N, Tu KP, Von Randow C. 2009. The land-atmosphere  
498 water flux in the tropics. *Global Change Biology* **15**: 2694-2714. DOI 10.1111/j.1365-  
499 2486.2008.01813.x.
- 500 Ford CR, Hubbard RM, Kloeppel BD, Vose JM. 2007. A comparison of sap flux-based evapotranspiration  
501 estimates with catchment-scale water balance. *Agricultural and Forest Meteorology* **145**: 176-  
502 185. 10.1016/j.agrformet.2007.04.010.
- 503 Foster PN. 2001. The potential negative impacts of global climate change on tropical montane cloud  
504 forests. *Earth-Science Reviews* **55**: 73-106.
- 505 Giesler LJ, Horst GL, Yuen GY. 1996. A site-specific sensor for measuring leaf wetness duration within  
506 turfgrass canopies. *Agricultural and Forest Meteorology* **81**: 145-156.
- 507 Gotsch SG, Asbjornsen H, Goldsmith GR. 2016. Plant carbon and water fluxes in tropical montane cloud  
508 forests. *Journal of Tropical Ecology* **32**: 404-420. 10.1017/S0266467416000341.
- 509 Gotsch SG, Asbjornsen H, Holwerda F, Goldsmith GR, Weintraub AE, Dawson TE. 2014. Foggy days and  
510 dry nights determine crown-level water balance in a seasonal tropical montane cloud forest.  
511 *Plant, Cell and Environment* **37**: 261-272.
- 512 Granier A. 1985. Une nouvelle methode pour la mesure du flux de seve brute dan the tronc des arbres.  
513 *Annales Des Sciences Forestières* **42**: 193-200.
- 514 Granier A, Huc R, Barigah ST. 1996. Transpiration of natural rain forest and its dependence on climatic  
515 factors. *Agricultural and Forest Meteorology* **78**: 19-29.
- 516 Granier A, Lostau D. 1994. Measuring and modelling the transpiration of a maritime pine canopy from  
517 sap-flow data. *Agricultural and Forest Meteorology* **71**: 61-81.
- 518 Green S, Clothier B, Jardine B. 2003. Theory and practical application of heat pulse to measure sap flow.  
519 *Agronomy Journal* **95**: 1371-1379.
- 520 Holdridge LR. 1967. *Life Zone Ecology, Rev. Ed. With Photographic Supplement Prepared by J. A. Tosi, Jr.*  
521 TROPICAL SCIENCE CENTER: San Jose, Costa Rica
- 522 Holwerda F, Alvarado-Barrientos MS, Gonzalez-Martinez TM. 2016. Surface energy exchange in a  
523 tropical montane cloud forest environment: Flux partitioning, and seasonal and land cover-  
524 related variations. *Agricultural and Forest Meteorology* **228**: 13-28.  
525 10.1016/j.agrformet.2016.06.011.
- 526 Horna V, Schuldt B, Brix S, Leuschner C. 2011. Environment and tree size controlling stem sap flux in a  
527 perhumid tropical forest of Central Sulawesi, Indonesia. *Annals of Forest Science* **68**: 1027-1038.  
528 DOI 10.1007/s13595-011-0110-2.
- 529 Houser C, Cahill A, Gonzalez E, Brooks S, Frauenfeld O, Miller G, Moore G, Rapp A, Roark B, Schade G,  
530 Schumacher C, Washington-Allen R, Brumbelow K, Lemmons K. 2013. Eco-Hydrology of a  
531 Tropical Montane Forest: A REU Site Hosted By Texas A&M University in Costa Rica. In: Annual  
532 ATBC-OTS Joint Meeting, San Jose, Costa Rica

- 533 Ilstedt U, Tobella AB, Bazie HR, Bayala J, Verbeeten E, Nyberg G, Sanou J, Benegas L, Murdiyarso D,  
 534 Laudon H, Sheil D, Malmer A. 2016. Intermediate tree cover can maximize groundwater  
 535 recharge in the seasonally dry tropics. *Scientific Reports* **6**: 1-12. DOI: 10.1038/srep21930.
- 536 Ishibashi M, Terashima I. 1995. Effects of Continuous Leaf Wetness on Photosynthesis - Adverse Aspects  
 537 of Rainfall. *Plant Cell and Environment* **18**: 431-438. DOI 10.1111/j.1365-3040.1995.tb00377.x.
- 538 Jasechko S, Sharp ZD, Gibson JJ, Birks SJ, Yi Y, Fawcett PJ. 2013. Terrestrial water fluxes dominated by  
 539 transpiration. *Nature* **496**: 347-351.
- 540 Jones HG. 1992. *Plants and Microclimate: A quantitative approach to environmental plant physiology*.  
 541 2nd edn. Cambridge University Press: Cambridge, U. K.
- 542 Kostner B. 2001. Evaporation and transpiration from forests in Central Europe - relevance of patch-level  
 543 studies for spatial scaling. *Meteorology and Atmospheric Physics* **76**: 69-82.
- 544 Kume T, Tanaka N, Kuraji K, Komatsu H, Yoshifuji N, Saitoh TM, Suzuki M, Kumagai T. 2011. Ten-year  
 545 evapotranspiration estimates in a Bornean tropical rainforest. *Agricultural and Forest  
 546 Meteorology* **151**: 1183-1192. 10.1016/j.agrformet.2011.04.005.
- 547 Kunert N, Aparecido LMT, Higuchi N, Santos J, Trumbore S. 2015. Higher tree transpiration due to road-  
 548 associated edge effects in a tropical moist lowland forest. *Agricultural and Forest Meteorology*  
 549 **213**: 183-192.
- 550 Kunert N, Aparecido LMT, Wolff S, Higuchi N, Santos J, Araujo AC, Trumbore S. 2017. A revised  
 551 hydrological model for the Central Amazon: the importance of emergent canopy trees in the  
 552 forest water budget. *Agr. Forest Meteorol.* **239**: 47-57.
- 553 Lane PN, Mackay SM. 2001. Streamflow response of mixed-species eucalypt forests to patch cutting and  
 554 thinning treatments. *Forest Ecology and Management* **143**: 131-142.
- 555 Loescher HW, Gholz HL, Jacobs JM, Oberbauer SF. 2005. Energy dynamics and modeled  
 556 evapotranspiration from a wet tropical forest in Costa Rica. *Journal of Hydrology* **315**: 274-294.
- 557 Loescher HW, Powers JS, Oberbauer SF. 2002. Spatial variation of throughfall volume in an old-growth  
 558 tropical wet forest, Costa Rica. *J Trop Ecol* **18**: 397-407. Doi 10.1017/S0266467402002274.
- 559 Magarey RD, Seem RC, Weiss A, Gillespie T, Huber L. 2005. Estimating surface wetness on plants.  
 560 *Agronomy & Horticulture - Faculty Publications* **696**: 199-226.
- 561 Malhi Y, Pegoraro E, Nobre AD, Pereira MGP, Grace J, Culf AD, Clement R. 2002. Energy and water  
 562 dynamics of a central Amazonian rain forest. *Journal of Geophysical Research-Atmospheres* **107**:  
 563 1-17. 10.1029/2001jd000623.
- 564 McJannet D, Fitch P, Fisher M, Wallace J. 2007. Measurements of transpiration in four tropical rainforest  
 565 types of north Queensland, Australia. *Hydrological Processes* **21**: 3549-3564. 10.1002/hyp.6576.
- 566 Meinzer FC. 2003. Functional convergence in plant responses to the environment. *Oecologia* **134**: 1-11.  
 567 DOI 10.1007/s00442-002-1088-0.
- 568 Meinzer FC, Goldstein G, Andrade JL. 2001. Regulation of water flux through tropical forest canopy  
 569 trees: Do universal rules apply? *Tree Physiology* **21**: 19-26.
- 570 Meinzer FC, James SA, Goldstein G. 2004. Dynamics of transpiration, sap flow and use of stored water in  
 571 tropical forest canopy trees. *Tree Physiology* **24**: 901-909.
- 572 Meinzer FC, James SA, Goldstein G, Woodruff D. 2003. Whole-tree water transport scales with sapwood  
 573 capacitance in tropical forest canopy trees. *Plant Cell and Environment* **26**: 1147-1155. DOI  
 574 10.1046/j.1365-3040.2003.01039.x.
- 575 Moore GW, Bond BJ, Jones JA, Phillips N, Meinzer FC. 2004. Structural and compositional controls on  
 576 transpiration in 40-and 450-year-old riparian forests in western Oregon, USA. *Tree Physiology*  
 577 **24**: 481-491.
- 578 Moore GW, Owens MK. 2012. Transpirational water loss in invaded and restored riparian forests of the  
 579 Rio Grande. *Restoration Ecology* **20**: 346-351.

- 580 Motzer T, Munz N, Kuppers M, Schmitt D, Anhuf D. 2005. Stomatal conductance, transpiration and sap  
 581 flow of tropical montane rain forest trees in the southern Ecuadorian Andes. *Tree Physiology* **25**:  
 582 1283-1293.
- 583 O'Brien JJ, Oberbauer SF, Clark DB. 2004. Whole tree xylem sap flow responses to multiple  
 584 environmental variables in a wet tropical forest. *Plant, Cell and Environment* **27**: 551-567.
- 585 Oliveira RS, Eller CB, Bittencourt PRL, Mulligan M. 2014. The hydroclimatic and ecophysiological basis of  
 586 cloud forest distributions under current and projected climates. *Annals of Botany* **113**: 909-920.  
 587 10.1093/aob/mcu060.
- 588 Oren R, Philips N, Ewers B, Pataki D, Megonigal JP. 1999. Sap-flux-scaled transpiration responses to light,  
 589 vapor pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest. *Tree  
 590 Physiology* **19**: 337-347.
- 591 Oren R, Philips N, Katul GG, Ewers BE, Pataki DE. 1998. Scaling xylem sap flux and soil water balance and  
 592 calculating variance: a method for partitioning water flux in forests. *Annales des sciences  
 593 forestières* **55**: 191-216.
- 594 Pataki DE, McCarthy HR, Litvak E, Pincetl S. 2011. Transpiration of urban forests in the Los Angeles  
 595 metropolitan area. *Ecological Applications* **21**: 661-677. Doi 10.1890/09-1717.1.
- 596 Phillips N, Nagchaudhuri A, Oren R, Katul G. 1997. Time constant for water transport in loblolly pine  
 597 trees estimated from time series of evaporative demand and stem sapflow. *Trees* **11**: 412-419.
- 598 Porporato A, D'Odorico P, Laio F, Ridolfi L, Rodriguez-Iturbe I. 2002. Ecohydrology of water-controlled  
 599 ecosystems. *Adv. Water Resour.* **25**: 1335-1348.
- 600 Pypker TG, Bond BJ, Link TE, Marks D, Unsworth MH. 2005. The importance of canopy structure in  
 601 controlling the interception loss of rainfall: Examples from a young and an old-growth Douglas-  
 602 fir forest. *Agricultural and Forest Meteorology* **130**: 113-129.
- 603 Reinhardt K, Smith WK. 2008. Impacts of cloud immersion on microclimate,photosynthesis and water  
 604 relations of *Abies fraseri* (Pursh.) Poiret in a temperate mountain cloud forest. *Oecologia* **158**:  
 605 229-238.
- 606 Ritter A, Regalado CM, Aschan G. 2008. Fog reduces transpiration in tree species of the Canarian relict  
 607 heath-laurel cloud forest (Garajonay National Park, Spain). *Tree Physiology* **29**: 517-528.
- 608 Roberts J, Gash JHC, Tani M, Bruijnzeel LA. 2005. Controls on evaporation in lowland tropical rainforest.  
 609 In: Bonell M, Bruijnzeel LA (eds) *Forests, Water and People in the Humid Tropics: Past, Present  
 610 and Future Hydrological Research for Integrated Land and Water Management*. Cambridge  
 611 University Press, New York, pp 287-313
- 612 Schuur EAG. 2003. Productivity and global climate revisited: The sensitivity of tropical forest growth to  
 613 precipitation. *Ecology* **84**: 1165-1170. Doi 10.1890/0012-9658(2003)084[1165:Pagcrt]2.0.Co;2.
- 614 Sentelhas PC, Monteiro JEBA, Gillespie T. 2004. Electronic leaf wetness duration sensor: why it should be  
 615 painted. *International Journal of Biometeorology* **48**: 202-205.
- 616 Teale NG, Mahan H, Bleakney S, Berger A, Shibley N, Frauenfeld OW, Quiring SM, Rapp AD, Roark EB,  
 617 Washington-Allen R. 2014. Impacts of Vegetation and Precipitation on Throughfall  
 618 Heterogeneity in a TropicalPre-Montane Transitional Cloud Forest. *Biotropica* **46**: 667-676.
- 619 Team RC. 2013. R: a language and environment for statistical computing. R Foundation for Statistical  
 620 Computing. In, Vienna, Austria
- 621 Trenberth KE. 1999. Atmospheric moisture recycling: Role of advection and local evaporation. *J Climate*  
 622 **12**: 1368-1381.
- 623 Washington-Allen RA, Moore GW, Buckwalter EH, Burns J, Dennis AR, Dodge O, Guffin EC, Morris ER,  
 624 Oien RP, Orozco G, Peterson A, Teale NG, Shibley NC, Tourtellotte N, Houser C, Frauenfeld OW,  
 625 Quiring SM, Roark B, Arnott R, Brooks SD, Rapp AD, Brumbelow JK, Cahill AT, Miller GR, Gonzalez  
 626 E, Hallmark CT, J.McInnes K, Morgan C, Ackerson JP, Delgado A. 2012. Exploratory Water Budget

- 627                  Analysis of A Transitional Premontane Cloud Forest in Costa Rica Through Undergraduate  
628                  Research. In: AGU Fall Meeting, San Francisco, California
- 629                  Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Groom PK, Hikosaka K, Lee W, Lusk CH, Niinemets Ü,  
630                  Oleksyn J, Osada N, Poorter H, Warton DI, Westoby M. 2005. Modulation of leaf economic traits  
631                  and trait relationships by climate. *Global Ecology and Biogeography* **14**: 411-421.  
632                  10.1111/j.1466-822x.2005.00172.x.
- 633                  Wullschleger SD, Hanson PJ, Todd DE. 2001. Transpiration from a multi-species deciduous forest as  
634                  estimated by xylem sap flow techniques. *Forest Ecology and Management* **143**: 205-213.
- 635                  Zhang K, Kimball JS, Nemani RR, Running SW. 2010. A continuous satellite-derived global record of land  
636                  surface evapotranspiration from 1983 to 2006. *Water Resour. Res.* **46**: W09522.  
637                  10.1029/2009wr008800.
- 638                  Zhang Q, Manzoni S, Katul G, Porporato A, Yang DW. 2014. The hysteretic evapotranspiration- Vapor  
639                  pressure deficit relation. *Journal of Geophysical Research-Biogeosciences* **119**: 125-140.  
640                  10.1002/2013jg002484.
- 641                  Zheng H, Wang QF, Zhu XJ, Li YN, Yu GR. 2014. Hysteresis Responses of Evapotranspiration to  
642                  Meteorological Factors at a Diel Timescale: Patterns and Causes. *PLoS One* **9**:  
643                  10.1371/journal.pone.0098857.
- 644

645

646 **Tables**

647 TABLE 1. Size classes for upscaling from sap flux density to watershed level transpiration based on  
 648 diameter at breast height (*DBH*).

649

<b>Size Class</b>	<b>Diameter range (cm)</b>	<b>Total Sapwood Area (m<sup>2</sup>)</b>		
		<b>Instrumented Plot</b>	<b>All Plots</b>	<b>Watershed Level</b>
Class 1	<i>DBH</i> ≤7.5	0.019	0.021	0.164
Class 2	7.5< <i>DBH</i> ≤17	0.076	0.144	1.12
Class 3	17< <i>DBH</i> ≤21	0.123	0.227	1.77
Class 4	21< <i>DBH</i> ≤33	0.222	0.504	3.92
<b>Class 5</b>	<b>33&lt;<i>DBH</i>≤240</b>	<b>0.768</b>	<b>6.02</b>	<b>46.8</b>

650

651

652 TABLE 2. Size and species of trees instrumented with sap flow sensors, ordered by diameter. \*indicates  
 653 tree individuals that underwent radial profile measurements. Size classes were based on diameter.

654

Size Class	Height (m)	Diameter (cm)	Sapwood Depth (cm)	Family	Genus	Species
1	6.1	4.2		Pyllanthaceae	<i>Phyllanthus</i>	<i>skutchii</i> Standl.
1	9.8	6.3		Asteraceae	<i>Koanophyllum</i>	<i>hylonum (B.L. Rob.) R. M. King &amp; H. Rob.</i>
1	11.1	7.4		Lacistemataceae	<i>Lozania</i>	<i>pittieri (S.F. Blake) L.B. Sm.</i>
2	8.4	10.6		Anacardiaceae	<i>Mosquitoxylum</i>	<i>jaimacense (Krug &amp; Urb.)</i>
2	11.1	15.8		Euphorbiaceae	<i>Pousandra</i>	<i>trianaee (Müll. Arg.) Baill.</i>
2	16.3	16.5		Melastomataceae	<i>Miconia</i>	<i>serrulata (DC.) Naud.</i>
3	10.1	16.9*	7.3	Malvaceae	<i>Helicocarpus</i>	<i>appendiculatus Turcz.</i>
3	15.8	19.2*	5.0	Myrtaceae	<i>Virola</i>	<i>koschnyi Warb.</i>
3	13.7	20.6		Eleocarpaceae	c.f. <i>Sloanea</i>	<i>sp.</i>
4	14.7	27.8*	9.0	Annonaceae	<i>Annona</i>	<i>macrocarpa (Wercklé.)</i>
4	10.4	27.8*	8.5	Fabaceae	<i>Inga</i>	<i>sp.</i>
4	16.4	32.8		Calophyllaceae	<i>Calophyllum</i>	<i>brasiliense (Cambess.)</i>
5	15.3	42.0*	9.0	Moraceae	<i>Brosimum</i>	<i>sp.</i>
5	15.3	43.8		Rubiaceae	<i>Chomelia</i>	<i>venulosa (W.C. Burger &amp; C.M. Taylor)</i>
5	35.4	119.9*	12.0	Meliaceae	<i>Carapa</i>	<i>guianensis (Aublet)</i>

655

656 **Figure Legends**

657 FIGURE 1. Monthly mean values with standard deviations for (a) air temperature, (b) solar radiation, (c)  
658 vapor pressure deficit, and (d) total rainfall for a two-year period that encompasses the sap flux  
659 measurement period from January 16 to November 14, 2012.

660

661 FIGURE 2. Stand inventory for our measurement site, including (a) the number of trees in each diameter  
662 class, (b) the relationship between basal area and sapwood area (for trees equipped with sap flow sensors  
663 and an additional 26 trees spanning the full range in diameters), and (c) the proportion of sapwood area in  
664 each diameter class (using the relationship in panel a to predict unmeasured trees).

665

666 FIGURE 3. Radial sap flux measurements. Relative flux was calculated by normalizing the value at a  
667 given depth,  $J_i$ , to the value in the outer 1 cm,  $J_{i=1}$ . Relative depth was calculated by normalizing the  
668 depth of each measurement,  $L_i$ , to the total sapwood depth,  $L_{sapwood}$ , measured via core sampling (Table  
669 1). Symbol colors range from light to dark grey according to tree diameter (d), see also Table 2.

670

671 FIGURE 4. Patterns of sap flux, solar radiation, and rainfall, along with understory and top of canopy leaf  
672 wetness and vapor pressure deficit (VPD) for two select days in June 2011, a dry day (DOY 178) and a  
673 wet day (DOY 181).

674

675 FIGURE 5. Daily stand transpiration (mm/d) in relation to average vapor pressure deficit (a) and  
676 incoming solar radiation (b) partitioned into classes 1 – 4 (dark gray) and class 5 (light gray).

677

678 FIGURE 6. Mean 10-minute sap flux density by tree size class (see Tables 1 and 2) for February (wet  
679 season) (a) and March (dry season) (b) of 2013.

680

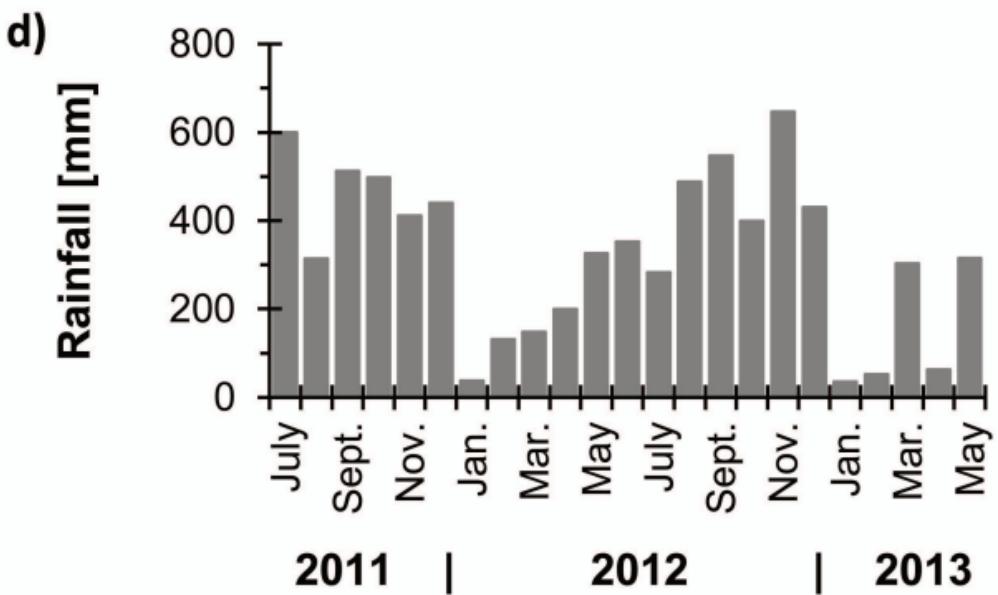
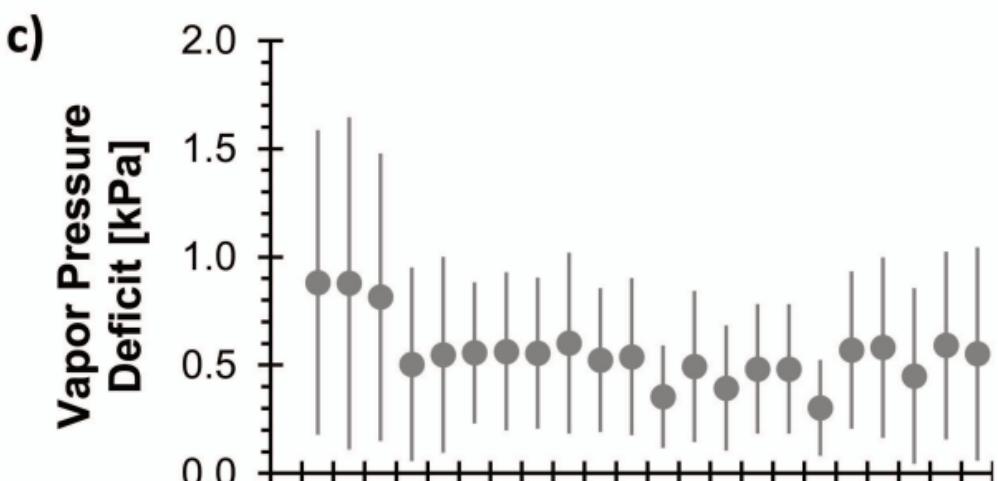
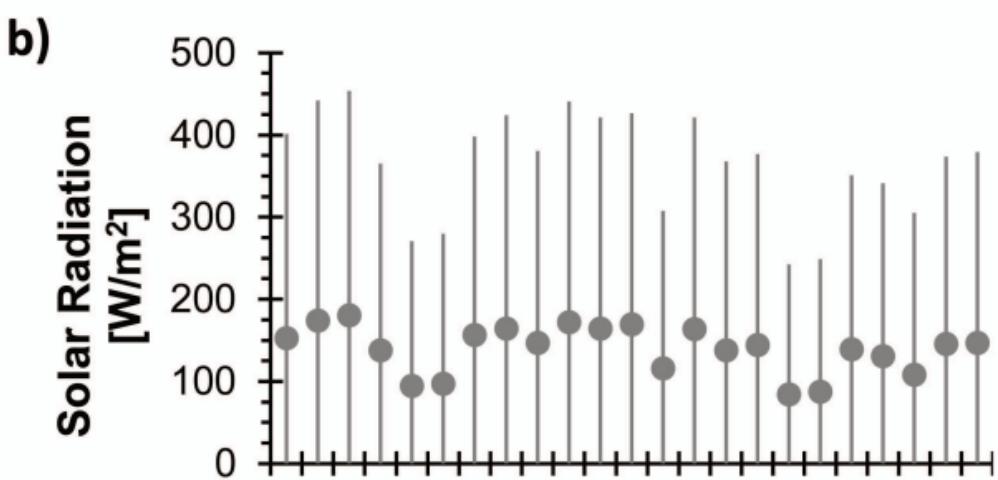
681 FIGURE 7. Diurnal patterns in vapor pressure deficit (a) and solar radiation (b) along with plots  
682 demonstrating hysteresis in the relationship between hourly average sap flux density and hourly averages  
683 of these variables, shown for classes 1 – 4 (c,d) and for class 5 (e,f). Peak sap flow rates occur near  
684 midday (labeled noon).

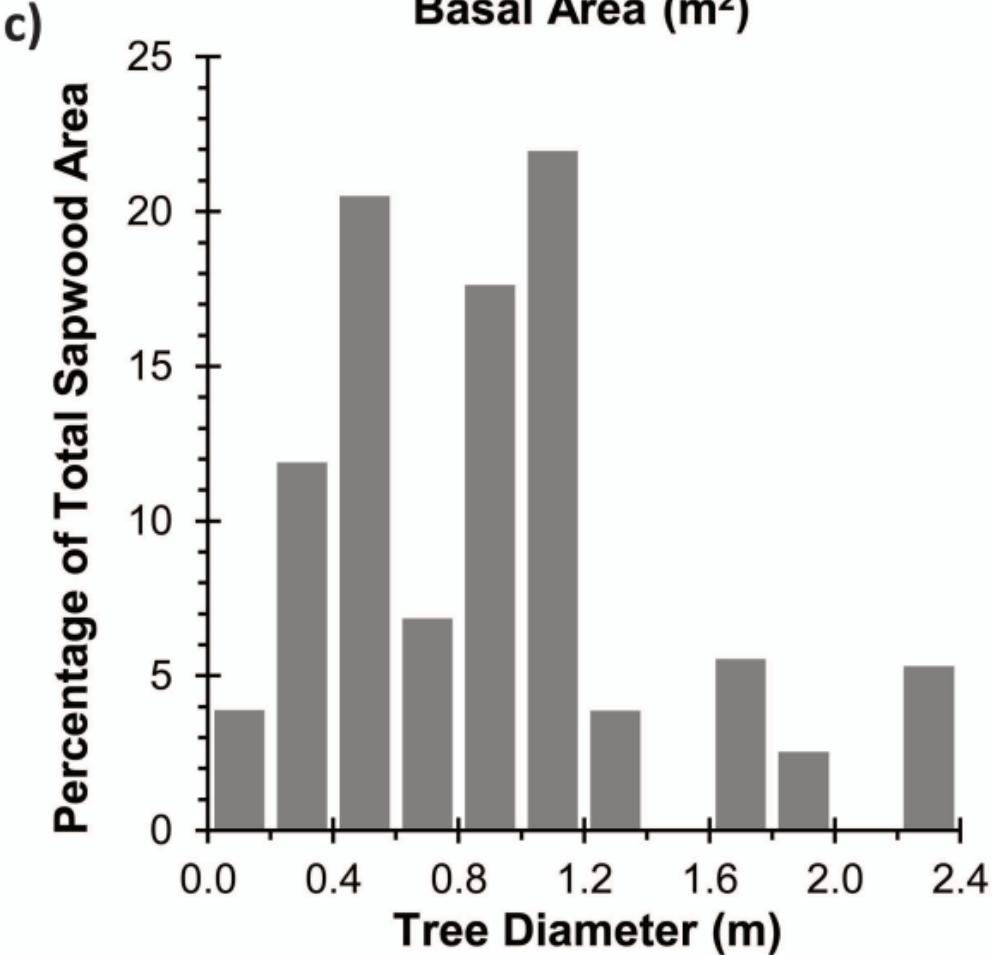
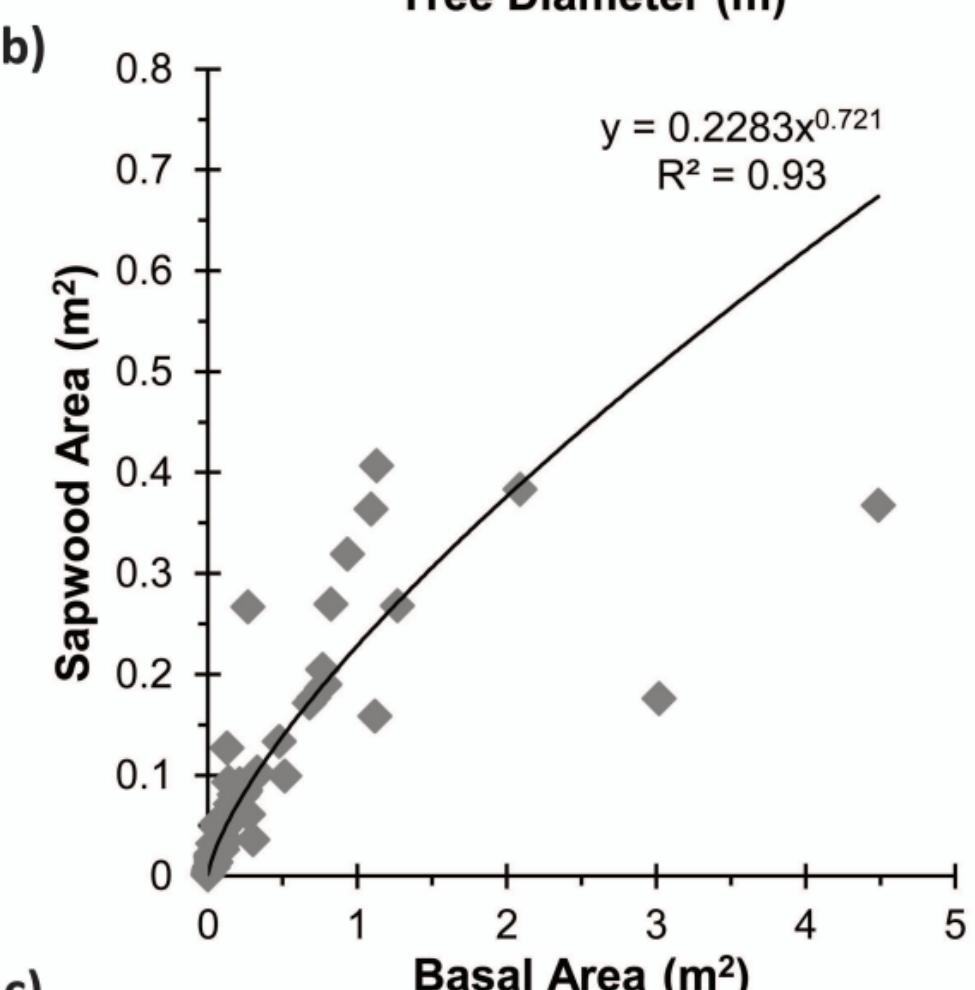
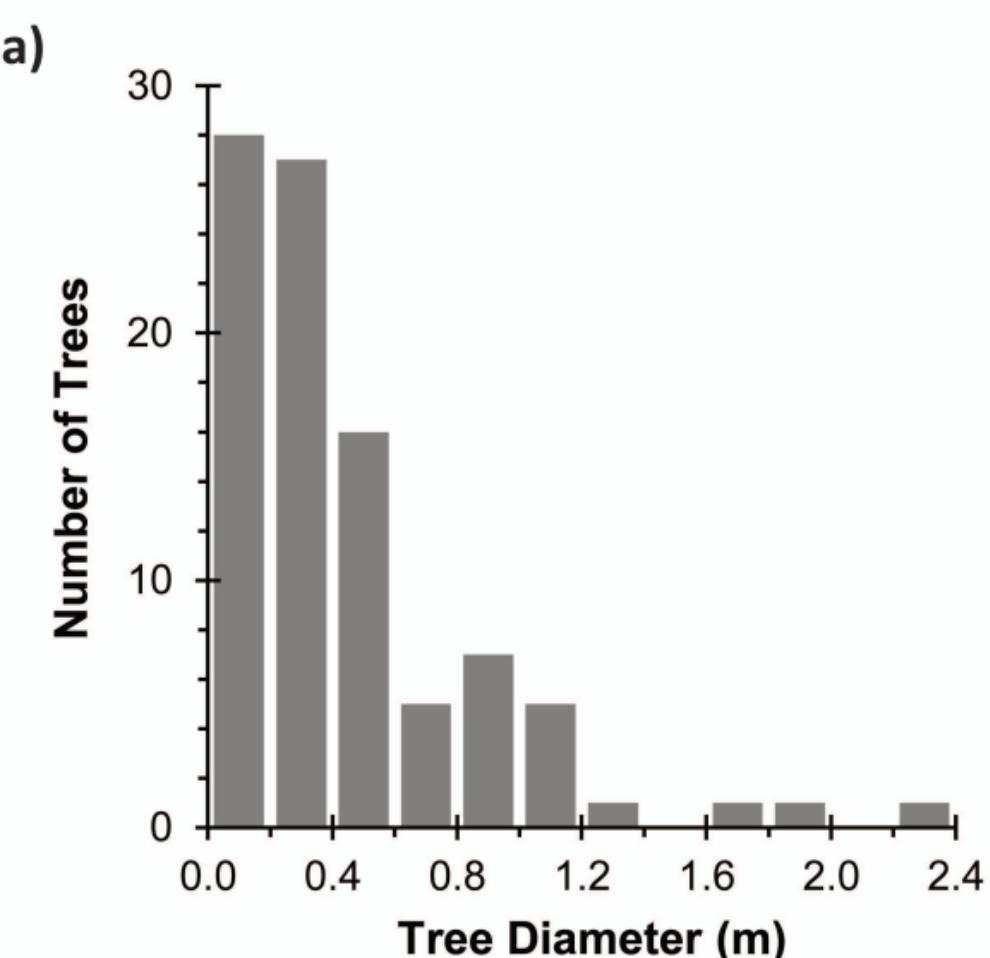
685

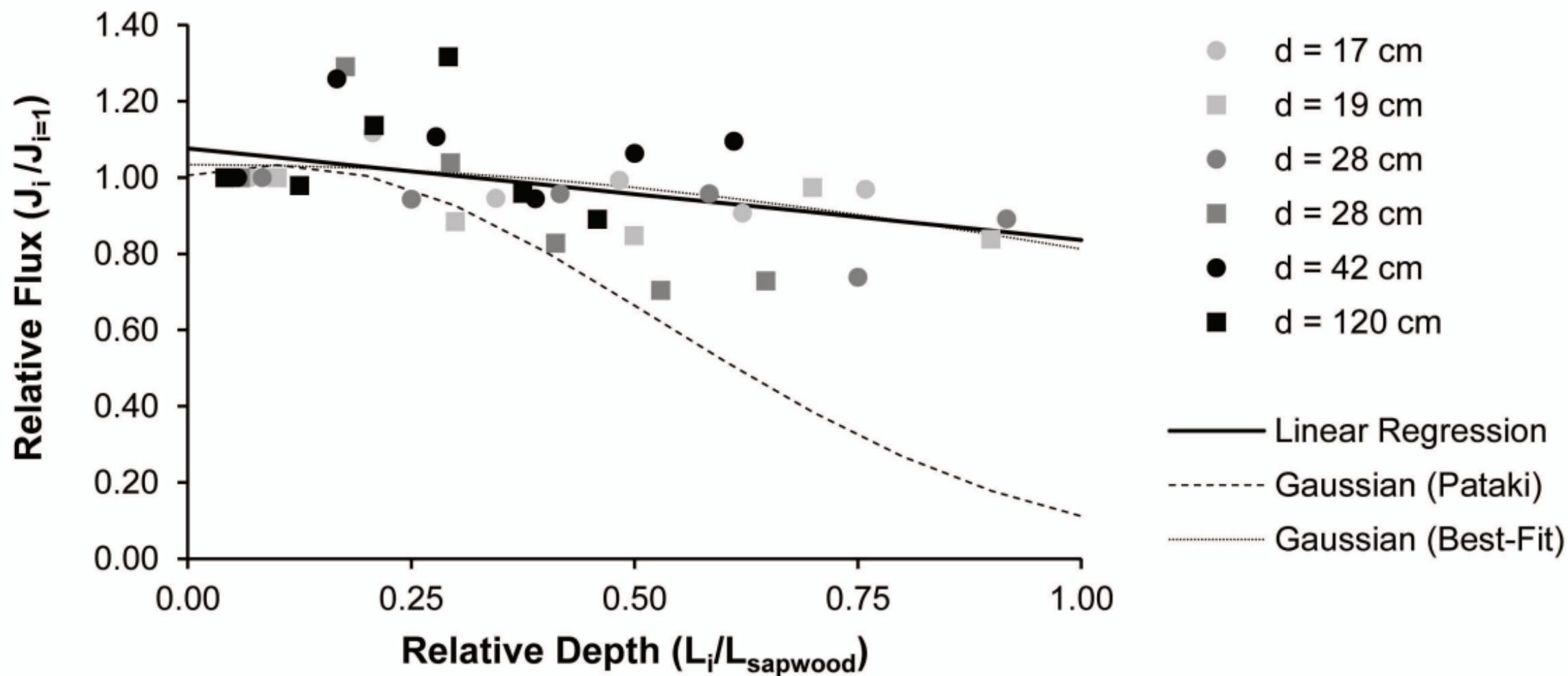
686 FIGURE 8. Sap flux density (a) and total tree water use (b) as a function of tree diameter. Following  
687 Holwerda *et al.* (2016), tree water use increased as a power function of diameter ( $y = ax^b$ ).

688

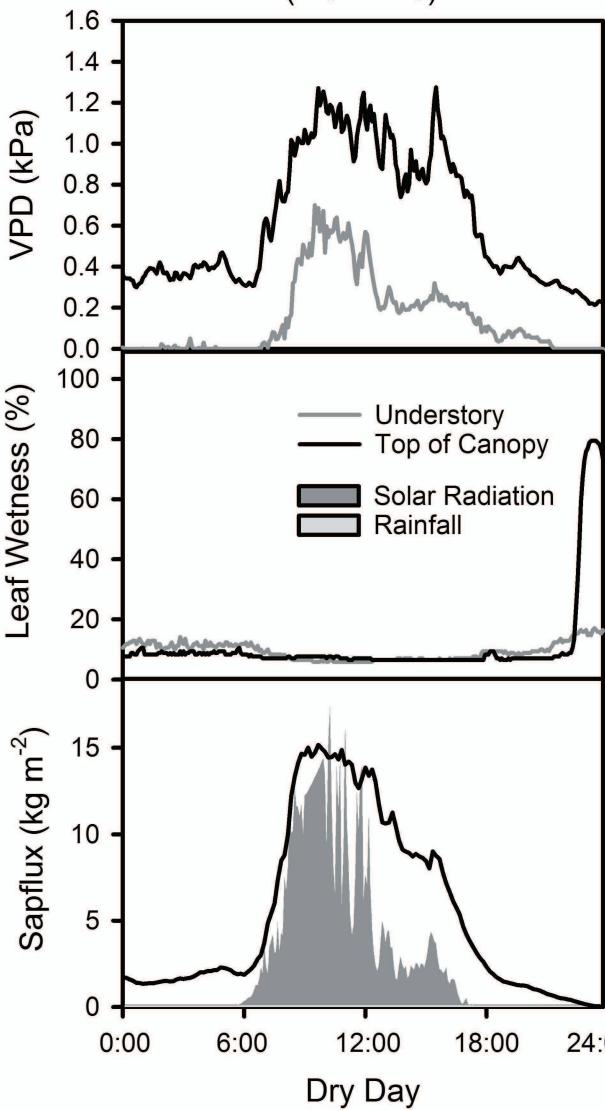
689 FIGURE 9. Contribution of 5 tree size classes to monthly total stand transpiration for the period of  
690 January 16 to November 14, 2012. Totals shown separately for classes 1 – 4 combined (dark gray) and for  
691 class 5 (light gray).







Dry Day  
(DOY 178)



Wet Day  
(DOY 181)

