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Dry Season Transpiration and Soil Water Dynamics in the Central Amazon

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Publication Date

2022

DOI

10.3389/fpls.2022.825097

Peer reviewed

Drought-driven shifts in tree water use linked to root distribution, sap flow and basal area in the Central Amazon

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27 **Keywords:** allometry, ecohydrology, root water uptake, soil water, transpiration, tropical forests

28

29 **Abstract**

30 With model projections of more intense and frequent droughts in the future, there is increasing
31 importance in understanding tree and stand-level water flux through tropical forest ecosystems during
32 dry periods. Here we investigate paired soil and tree water extraction dynamics in an old-growth terra-
33 firme forest in central Amazonia during the driest period of 2018. Species-specific tree water use was
34 assessed via radial patterns of sap flow in eight dominant canopy trees with a range in diameter, height
35 and wood density. Paired multi-sensor soil moisture probes were installed adjacent to six of those trees

36 and quantified volumetric water content dynamics at 10, 20, 30, 40, 50, 70 and 100 cm. To link depth-
37 specific water extraction patterns to root distribution, fine root biomass was also assessed through the
38 soil profile to 2.35 m. To scale water extraction to the plot level, basal area was measured for all trees
39 within a 5 m radius around each soil moisture probe. The sensitivity of tree transpiration to drought
40 varied by species, with some increasing and some decreasing water use during the dry period. Tree-level
41 water use broadly scaled with sapwood area across species, from 11-190 liters per day. Plot level water
42 use increased linearly with plot basal area, indicating daily transpiration from ~1.7 to 3.3 mm per day,
43 depending on spatial location. Upper soil water extraction was strongly dependent on root biomass,
44 which was dense at the surface (i.e., 45% in the upper 5 cm) and declined dramatically with depth. Yet
45 as the upper soil dried, water extraction shifted to deeper levels and model projections suggest that much
46 of the water use during the month-long dry-down could be extracted from the upper 2 m. Results
47 indicate wide variation in soil water extraction temporally in both the vertical and horizontal directions.
48 The results provide key information on the species-specific regulation of transpiration by dominant trees
49 as water availability changes and the simultaneous dynamics of soil water extraction that can be used to
50 inform mechanistic models that project tropical forest response to drought.
51

52 **Introduction**

53 The response of tropical forest transpiration (T) to changes in environmental conditions remains highly
54 uncertain in Earth System Models due to an unresolved understanding of both abiotic and biotic factors
55 and their interactions (e.g., Berg and Sheffield 2019). Uncertainty is amplified by the high trait diversity
56 of tropical trees (Cardoso et al., 2017) and their differential responses to drought conditions (Cox et al.,
57 2004; Baker et al., 2008; Malhi et al., 2009). Within tropical forests, ecosystem T is mediated by tree
58 size, and species-specific traits including stomatal sensitivity to leaf water loss driven by vapor pressure
59 deficit (VPD) (Fontes et al. 2018, Barros et al. 2019, Gimenez et al. 2019, Grossiord et al. 2019). In the
60 Amazon rainforest, studies have reported both drought-induced increases (da Rocha et al. 2009; Brum et
61 al. 2018) and decreases (da Rocha et al., 2009; Fontes et al., 2018) in the rate of T. While we know that
62 forest evapotranspiration is influenced by dominant abiotic factors including net radiation, boundary
63 layer conductance and VPD (Costa et al., 2010, Brum et al. 2018, Grossiord et al. 2019), it is plant
64 available water which may explain why evapotranspiration is limited in some regions of the Amazon,
65 but not in others (Fisher et al. 2008, Grossiord et al. 2019).
66

67 In the central Amazon, where rainfall is high and the dry season is usually less than four months,
68 evapotranspiration generally follows climatic conditions (da Rocha et al., 2009) but can become limited
69 during drought conditions (Fisher et al., 2008). Moreover, given the low soil water holding capacity of
70 the Oxisols that are common in central Amazon, only a short sequence of days without precipitation can
71 lead to the depletion of near surface soil water and as a result, a greater depth of soil has to be exploited
72 to maintain root water uptake (Hodnett et al., 1995). In the central Amazon, most root distribution is in
73 the upper 20 cm (Ferreira et al., 2002; Noguchi et al., 2014), yet water absorption has been exhibited to
74 at least 3.6 meters (Hodnett et al., 1995, 1996), and there is evidence of rooting to 6-10 m depths
75 (Chauvel et al., 1992, Negrón-Juárez et al., 2020). Further east in Pará state, Brazil, tree roots have been
76 found to depths of 18 m (Nepsted et al. 1994).
77

78 Differences in access to and use of water are often dependent on tree height and diameter (West et al.
79 1997, Meinzer et al. 2005). Diameter can be used to predict characteristics related to hydraulic capacity
80 such as sapwood area (Aparecido et al. 2019), which can then be used to estimate whole tree water use if
81 sap velocity is known. In the tropics, the largest, emergent trees are subject to greater evaporative

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82 demand than other canopy trees (Kunert et al., 2017; Motzer et al., 2005) and are a major source of
83 stand-level T (Brum et al. 2018). Yet, for dominant and emergent trees to maintain T and photosynthesis
84 during drought requires that they leverage appropriate hydraulic strategies. Amongst these, root access
85 to deeper water sources is one trait that the largest trees display (da Rocha et al., 2004; Lee et al., 2005;
86 Oliveira et al., 2005; Bruno et al., 2006), although some smaller trees have also been shown to access
87 deeper water sources (e.g., Stahl et al. 2013).

88

89 Other traits also influence transpiration dynamics, including relative hydraulic conductivity through the
90 xylem pathway (Fisher et al. 2006) and stomatal sensitivity to internal water availability and external
91 driving forces (Meinzer 2002, Gimenez et al. 2019). Under drying conditions, tropical trees display a
92 variety of responses, including avoidance (e.g., leaf drop, or reducing water use by closing stomata –
93 more conservative strategy) or tolerance (e.g., maintaining water use at the risk of hydraulic failure –
94 more acquisitive strategy). Either strategy may ultimately contribute to mortality under excessive
95 drought due to either carbon starvation or hydraulic failure (Rowland et al., 2015; McDowell et al. 2018
96 Aleixo et al., 2019;). Understanding species-specific variation in T and its response to drought,
97 therefore, lends insight into relative hydraulic strategies and how they may manifest at the stand level.
98 Knowledge of functional traits and how those traits scale with size can thus provide a pathway for
99 process-level understanding of the controls regulating ecosystem dynamics, including T (e.g., Kotowska
100 et al. 2021). Such data can be highly useful for forest and ecosystem modeling efforts (e.g., Scheiter et
101 al. 2013, Christoffersen et al. 2016).

102 *Objectives*

103 The objective of this work was to better understand the seasonal patterns of tree water use as linked to
104 upper soil water availability during a dry period in terra-firme soils of the Central Amazon. Our specific
105 questions are: (1) Do different co-occurring canopy species increase or decrease water use during
106 drought, when atmospheric demand for water is increasing but upper soil water supply is declining? (2)
107 As soils dry, does tree water extraction shift to deeper layers? (3) Can we predict T based on tree size,
108 stand basal area or soil water content in the upper 1 m? Results will provide key insights into the
109 species-specific regulation of T by dominant trees as water availability changes, and concurrent
110 dynamics of soil water extraction that can be used to inform models of tropical forest response to
111 drought.

112 **Material and methods**

113 *Study area*

114 The study was conducted at the ZF-2 Tropical Forestry Experimental Station (02°36'33"S; 60°12'33"W;
115 ~130 m elevation) within the Biological Reserve of Cuieras in Central Amazon. According to Koppen's
116 classification the climate is type Af (Tropical) with a short dry season that generally occurs between July
117 and September (Alvarez et al. 2013; Wu et al. 2016). The temperature ranges from 26.8 °C and 28.8 °C
118 but can reach up to 31 °C (Miranda et al. 2002). The predominant soil type in the plateau areas is the
119 dystrophic yellow latosol (Chauvel et al., 1992), an Oxisol. This is a very clayey soil with clay contents
120 that increase from 59% at the surface to 73% at 1 m depth, with an average porosity of about 0.58 m³ m⁻³
121 ³. Wilting point to field capacity ranged from ~0.27 to 0.41 m³ m⁻³ for the upper 1 m depth (Chauvel et
122 al., 1992; Marques et al. 2004). The closed-canopy primary forest is located on a plateau (terra-firme)
123 with heterogeneous tree sizes, ages and canopy heights (Oliveira et al., 2008). Most of the crowns are
124 globular in shape, with little direct radiation entering in lower strata. Although the height of individuals

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125 varies widely, more than 50% are between 14 and 25 m, with emergent trees reaching up to 50 m
126 (Oliveira et al., 2008). Estimates of tree age based on carbon isotopes for 20 species in the area ranged
127 from 200 to 1,400 years (Chambers et al., 1998).

128 *Micrometeorological variables*

129 Micrometeorological variables were obtained from the 50 m K-34 tower managed by the Large-Scale
130 Biosphere-Atmosphere Program – LBA (Araújo et al., 2002). Precipitation was measured by a rain
131 gauge (EM ARG100, Environmental Measurements Limited, UK) and air temperature (T_{air}) and relative
132 humidity (R_{H}) were obtained by means of a thermo-hygrometer (HMP45AC, Vaisala, Finland) at 28 m
133 height. Vapor pressure deficit (VPD) was derived from T_{air} and R_{H} using Tetens equation. All
134 micrometeorological variables were collected at a 30-minute time frequency.

135 *The Accumulated Daily Water Deficit*

136 As in most humid tropical forests, precipitation events during the dry season are common. We used the
137 accumulated daily water deficit (ADWD; e.g., Santos et al. 2018) metric to delimit the dry period.
138 Similar to the cumulative water deficit and maximum cumulative water deficit metrics (Malhi et al.,
139 2009), the ADWD measures the duration and intensity of a drought using daily precipitation (Santos et
140 al., 2018). ADWD is calculated using the cumulative precipitation from the previous 30 days and a dry
141 period occurs when this cumulative is less than the average monthly forest evapotranspiration (~100
142 mm) (Malhi et al., 2009; Santos et al., 2018). To reinforce the delimitation of the dry period, we also
143 compared the ADWD calculations to declines in soil water content and increases in VPD.

144 *Species selection*

145 For this study, eight dominant canopy tree species were selected for sap flow monitoring and six of these
146 were additionally paired with soil water sensors to quantify water extraction (Figure 1; Table 1). These
147 species were selected because they are generally abundant in this forest stand (Oliveira et al., 2008) and
148 individuals were located close to one another and adjacent to the K-34 flux tower. We selected one
149 individual tree per species. For each tree, we measured DBH at a height of 1.3 m from the ground and
150 height (HT) using a laser rangefinder (Trupulse, Laser Technology, Inc, USA) targeting the most
151 emergent branch. We also estimated canopy area (CA) as the average of the canopy diameters measured
152 from the forest floor in the north-south and east-west axes. To upscale T, we measured the DBH of all
153 trees within a 10 m diameter plot of the soil water sensors depicted in Figure 1; this included the
154 dominant sap flow tree, and smaller diameter (> 5cm DBH) trees and lianas within the plot.

155 *Sap velocity, sapwood area, and sap flow*

156 To calculate water use or sap flow (Q) of each of the eight trees, we measured radial patterns of sap
157 velocity (v_s), sapwood depth (SPD) and sapwood area (SA) (Table 1). The SPD was measured in the
158 field using a dye injection technique based on Goldstein et al. (1998). Briefly, a small ~6.5 mm hole was
159 drilled at 1.3 m through the sapwood at a slight downward angle through the sapwood into the
160 heartwood, and subsequently filled completely with dye (aqueous acid fuchsin filtered to 0.2 μm) under
161 slight pressure. The dye was retained in a 30 ml syringe reservoir held in place by its tip inserted through
162 the outer bark and phloem tissue. Additional dye was added as needed. After 1-2 h, an increment core
163 was collected ~2-3 cm above each dye injection point and the conductive sapwood tissue depth was

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164 determined from the thickness of the xylem wood where dye was visible. From *SPD*, we calculated the
165 total *SA* assuming that *SPD* was homogeneous across the trunk cross-section.

166
167 To measure v_s , we used heat dissipation-type sensors with a 2-cm sensing tip (TDP-GS, PlantSensors,
168 Australia; Granier, 1987). For each tree, the probes were installed at 1.3 m height at depths of 0-2 cm, 2-
169 4 cm, 4-6 cm and 6-8 cm (depending on dye-estimated sapwood depth) within active sapwood to
170 account for radial variation (Meinzer, Goldstein and Andrade, 2001). Each sensor consists of a set of
171 two temperature probes inserted into brass tubes, which protect the probes and provide good conduction
172 with the surrounding xylem. The two probes were separated by a vertical distance of 10 to 15 cm. The
173 upper probe was continuously heated, with 0.2 W, while the lower probe was used as a reference
174 temperature. The difference in temperature (or voltage) between the two probes was used to calculate v_s
175 (Oishi, Hawthorne and Oren, 2016) as:

$$v_s = aK^b \quad (1)$$

177 Where v_s is the sap velocity ($\text{g cm}^{-2} \text{s}^{-1}$), a is a universal empirical calibration coefficient (0.0119), b is the
178 exponent of the scale (1.23) and K is the temperature difference between the two sensors. While studies
179 have found the calibration coefficient does not represent all species (e.g., Bush et al., 2010), it has
180 proved appropriate in some tropical trees (e.g., McCulloh et al., 2007) and for this study, we assumed
181 the calibration coefficient was suitable for our trees. K is calculated by:

$$K = \frac{\Delta T_{max}}{\Delta T} - 1 \quad (2)$$

183 Where ΔT is the temperature difference between the heated and unheated probe, and ΔT_{max} is the
184 temperature difference between the two probes at zero flow, which is assumed to be reached on nights
185 with low VPD and dew formation on foliage. Then, we upscaled v_s to whole tree-level sap flow (Q ; g s^{-1})
186 by summing v_s for each concentric ring of active sapwood depth (i):

$$Q = \sum_{i=1}^{SPD} v_{si} \times SA_i \quad (3)$$

187 Where SA is the sapwood area (cm^2) at each sensor position into the sapwood (0-2 cm, 2-4 cm, 4-6 cm,
188 6-8 cm) until maximum depth (*SPD*) is reached (Table 1). Since some of the innermost sap flow sensors
189 partially extended into non-functional xylem, the integrated signal at that depth could be lower than
190 exists in the adjacent functional sapwood and may create some underestimation of sap flow at this depth,
191 although lower inner sap flow reduced the magnitude of this error.

192 *Allometric relationships and upscaling transpiration*

193 To describe the response of Q to drought, we focused our calculations on the most severe dry period as
194 defined by the ADWD. The trajectories of water use during this period were analyzed by linear
195 regressions and Q was normalized as a function of dry days. We only used days with high evaporative
196 demand, defined here as days with VPD > 1 kPa, exclude wet days or those with low evaporative
197 demand and likely with low water use.

198

199 Then, we upscaled Q to plot-level T . To do so, we first modeled tree-level SA vs DBH . We pooled data
 200 from our eight trees with additional allometry data collected by Aparecido et al. (2019) at the same site.
 201 In Aparecido et al. (2019), the relationship between SA and DBH was limited to trees with $DBH < 40$
 202 cm. In our study, the DBH of individual trees within the plot ranged from 29.8 to 113.8 cm, and 5 trees
 203 had a $DBH > 40$ cm. To avoid excessively weighting outliers, we applied Cook's method (Belsley et al.,
 204 1980; Cook and Weisberg, 1982) to detect potential outliers within the pooled data. We detected two
 205 outliers: *Buchenavia grandis*, which was the largest tree and *Ocotea nigrescens*, which had the largest
 206 sapwood area (Table 1). Removing these two outliers resulted in the highest correlation coefficient of SA
 207 vs. DBH , as compared to the total dataset or the dataset minus each outlier, and results were used to
 208 improve the Aparecido et al. (2019) allometric equation (Figure S1). In this way, we had a method to
 209 estimate SA based on DBH . Second, we used our eight species with sap flow sensors to draw a
 210 relationship between Q and SA and then calculated Q based on DBH . Then we upscaled Q to plot-level
 211 T according to:

$$T = \sum_{i=1}^n Q_i \quad (4)$$

212
 213 Where T is the summed transpiration for all trees (n) within the 10 m diameter plot and Q_i represents the
 214 Q of each tree in the plot estimated based on the two allometric relationships: Q vs SA and SA vs DBH .
 215 Plot level T could then be directly related to plot level basal area. The six plots were centered on each of
 216 the soil moisture probes that were installed one meter away from six of the sap flow trees (Figure 1).
 217 We compared this estimate of plot level T (Eq. 4) to measured sap flow of the dominant tree (Eq. 3) in
 218 each plot. Because T is at the plot level, we could then compare T to the water extraction measured by
 219 the soil water sensors.

220 Volumetric soil water content

221 For six of the eight sap flow trees, we measured volumetric soil water content (Figure 1; Table 1) using
 222 multi-frequency domain capacitance probes (FDC; EnviroSMART, Sentek Pty. Ltd, Stepney SA,
 223 Australia). The FDC probes were inserted into PVC access tubes located at 1 m distance from each tree.
 224 Initial installations reached 235 cm depth, however poor upper soil contact with the access tubes due to
 225 compaction required careful re-installations to 1 m depth. Soils from the initial installations were used for
 226 root assessment (described below). Each probe consisted of seven sensors spaced at different vertical
 227 intervals centered at depths 10, 20, 30, 40, 50, 70 and 100 cm, recording into a datalogger (model
 228 CR1000, Campbell Scientific Inc, Logan Utah USA) at 15- minutes intervals. Each sensor provides an
 229 integrated vertical measurement spanning ~10 cm; e.g., the sensor at 10 cm represents the 5-15 cm layer.
 230 The output of the FDC sensors is a dimensionless frequency that is converted using a normalization
 231 equation and then applied to a soil type-specific calibration equation by
 232

$$\theta = \frac{f}{A} + B + C \quad (5)$$

233
 234 Where f is the scaled frequency sensor output; θ is the volumetric water content ($m^3 m^{-3}$); A , B and C are
 235 the empirical coefficients of the equation. We initially used a calibration equation for a heavy cracking
 236 clay soil in Australia ('Warren' clay type, Sentek Calibration Manual, Sentek Pty Ltd), with calibration
 237 coefficients: $A = 0.0254$, $B = 1$, $C = -0.150$ (see the equations 1 and 2 below). This calibration resulted
 238 in reasonably, but slightly less absolute θ than other estimates at the site, thus we performed a site-
 239 specific calibration.
 240

241 Since the primary focus of this study was to examine relative changes in soil water content, errors in the
242 absolute calibration of the FDC sensors had minor impact on estimates of daily extraction rates. Even so,
243 we adjusted the default factory calibration based on soil texture and using a site-specific calibration. For
244 calibration, two access tubes were installed and allowed to equilibrate for four months, then a vertical
245 FDC sensor was inserted into the tube and the volumetric water content using the ‘Warren’ type heavy,
246 cracking clay (Sentek Calibration Manual; Sentek Pty Ltd 2001) was recorded. Immediately after
247 inserting the FDC sensor, 5 cm tall metal Kopecky rings were carefully pushed vertically into the soil
248 adjacent to the access tube. Each ring was carefully excavated, excess soil was cleaned off using a knife,
249 then they were immediately wrapped in plastic for subsequent wet and dry gravimetric measurements.
250 Based on these weights, volumetric water content was calculated as the mass of water divided by ring
251 volume. Two replicate samples with seven depths were collected along either side of the tube down to
252 ~60 cm. Some animal burrows and soil compaction affected several of the measurements, and two
253 samples were identified as outliers based on their interquartile range. The calibration regression between
254 actual and FDC θ ($R^2 = 0.71$) was then used to calculate f of the capacitance sensors from equation 5.
255 Data were then used to back calculate a new calibration equation with coefficients $A = 0.03154$, $B = 1$, C
256 $= -0.6349$, which can be used to convert f to VWC. There was one layer, 45-55 cm, that showed distinct
257 physical differences from other layers above and below. This included lower bulk density (1.01 ± 0.02
258 g cm^{-3} as compared with $1.18 \pm 0.04 \text{ g cm}^{-3}$ for other layers in the upper 1 m) and a siltier texture (22%
259 silt as compared with 4 - 6% for other layers in the upper 1m) and a lower clay content (64% as
260 compared with 80% for adjacent layers). Texture was quantified by the pipette method at the Soil and
261 Plant Analysis Laboratory (LASP) of Embrapa Amazônia Ocidental, Manaus, Brazil. The differences in
262 soil properties in the 45-55 cm layer result in greater macroporosity and water availability, which has
263 been previously identified by other studies in the area (e.g., Tomasella and Hodnett 1996; Broedel et al.
264 2017). For this layer, the heavy clay calibration resulted in low estimates of water content. As such, for
265 the 45-55 cm layer we used the manufacturer’s default calibration ($A = 0.1957$; $B = 0.404$; $C =$
266 0.02852).

267 *Fine root biomass*

268 In order to measure fine root biomass distribution, soil samples of a known volume were collected from
269 the same locations as the FDC soil water sensors (Figure 1; Table 1). Soil was excavated at
270 progressively larger depth intervals, initially at 5 cm intervals for the root-dense upper soil, to a 35 cm
271 interval at 200-235 cm. In the field, soils were stored in plastic bags to be transported to the Forest
272 Management Laboratory at the National Institute of Amazonian Research. In the lab, roots were
273 separated manually using steel mesh sieves of various diameters and tweezers. Only the roots with a
274 diameter < 2 mm were retained; black roots which had died and decayed were discarded (Vogt and
275 Persson, 1991). The fine roots were placed in paper bags and dried at 65°C for more than 48 hours until
276 constant weight was obtained.

277
278 Root biomass was summed by layer and for the entire 235 cm profile. Given the high diversity of
279 species, we did not separate roots by species, nor did we measure fresh root length. To describe fine root
280 biomass distribution, we fitted a non-linear model to fine root biomass and cumulative fraction as a
281 function of soil depth ($Y=1 - \beta^d$; where Y = cumulative root fraction at d =depth; Gale and Grigal, 1987).

282 *Soil water extraction*

283 Change in soil water content during the dry period was calculated as the difference in the initial and final
284 volumetric soil water content during each 15-minute interval for each of the six probes. Soil water

285 extraction from the upper 1 m was then estimated as the daily sum of the change in water content for
 286 each layer. At depths without sensors (e.g., 60 cm), data were interpolated based on the adjacent sensors
 287 (at 50 and 70 cm). In this study, evaporation at the soil surface was assumed to be zero since the dense
 288 forest canopy greatly limits solar radiation to the forest floor, as demonstrated by other studies in the
 289 Central Amazon (Kunert et al., 2017; Salati and Vose, 1984). Thus, the change in soil water content over
 290 the defined dry period was attributed exclusively to root water uptake. To relate fine root biomass to soil
 291 water extraction up to 1 m depth, we used a non-linear Michaelis-Menten type regression: $V = V_{\max} (R_d /$
 292 $(K_m + R_d))$, where V = extraction rate, R_d = root density and K_m = rate constant. Since tree water
 293 extraction can shift to deeper depths during drying periods, we also fit a logarithmic function of soil
 294 water extraction by soil depth to project potential water extraction to 2 or 3 m depth. The logarithmic fit
 295 allowed for an alternate estimate of plant water use for depths > 1m. The logarithmic fit also provided an
 296 estimate of water extraction between 0-10 cm depth at the beginning of the dry period. At the end of the
 297 dry period, it is likely that uptake was limited at this layer, and thus uptake was set to decline to zero at
 298 the surface. To compare water extraction as the soil dried, we performed the Student's t test when the
 299 data were normal, and the Wilcoxon test when data were not normal. Normality was checked with the
 300 Shapiro-Wilk test. Lastly, we compared soil water extraction to plot-level T upscaled using tree
 301 allometric relationships.

302 **Results**

303 *The Accumulated Daily Water Deficit*

304 The longest ADWD period in 2018 was from October 2nd to 20th, with a cumulative water deficit of 31
 305 mm (Figure 2A). During this two-week dry-down, the highest VPD values were observed, as well as the
 306 lowest soil water at 1 m, making ADWD a good metric to be used to characterize drought intensity. We
 307 also included the previous two weeks (September 16th to October 1st), as they represented initial pre-
 308 drought conditions with relatively low rainfall and soil water, and high VPD (Figure 2B-D). However,
 309 we discarded the last four days (October 17th to 20th) because a series of significant rain events caused an
 310 increase in soil water and a drop in VPD (Figure 2B-D). Therefore, we defined the dry period as
 311 September 16th to October 16th, 2018 (shading in Figure 2).

312 *Species-specific water use trends during the dry period*

313 For all species, sap velocity was greatest in the outer 2 cm of sapwood, ranging from about 6-30 cm h⁻¹,
 314 depending on species (Figure S2a,b). For trees with deeper sapwood, sap velocity declined with depth,
 315 with minimum values by 6 cm depth, and no sap flow at 8 cm depth. Sap velocity at different depths
 316 declined, remained flat, or increased over the course of the dry period, depending on species. During the
 317 dry period, Q varied by species (Figure 3; Table 2). Some species increased water use in response to the
 318 drought, some remained unchanged, while others reduced water use during the drought. Species which
 319 showed an increasing trend in daily water use as the dry period progressed were *Buchenavia grandis*,
 320 *Eschweilera romeu-cardosoi*, *Maquira sclerophylla* and *Ocotea nigrescens*. Species which showed a
 321 declining trend in daily water use during the same dry period include *Eriotheca globosa*, *Goupia glabra*
 322 and *Scleronema micranthum*, while *Swartzia recurve* remained constant. There was a wide range in
 323 species-specific water use, from ~11 liters day⁻¹ for *S. recurva*, up to 190 liters day⁻¹ for *O. nigrescens*
 324 (Table 2).

325 *Soil water extraction by depth*

326 We determined soil water extraction based on changes in the volumetric soil water content over time at
 327 each depth. For the duration of the dry period, the average water extracted from the upper 1 m was 0.86
 328 ± 0.15 mm day⁻¹, ranging from 0.67 to 1.01 mm day⁻¹. We found temporal differences in the total water
 329 extracted from top 1 m of soil (t-test; df=5, p=0.02). At the beginning of the dry period soil water
 330 extraction was 0.94 ± 0.09 mm day⁻¹, but then decreased to 0.74 ± 0.07 mm day⁻¹ by the end of the dry
 331 period (Figure 4). We also found differences in the vertical pattern of water extraction within the top 1 m
 332 of soil. Rates of water extraction declined with depth as both the root biomass declined and there was a
 333 change in soil texture; extraction rates declined as sand content declined from ~18% in the upper layer to
 334 12% at 1 m depth ($R^2 = 0.93$). At the start and end of the dry period, water extraction was consistently
 335 greatest in the shallow soil layers. However, as the drought progressed, the rate of extraction declined
 336 for the upper layers, and increased for the deeper soil. Using the logarithmic function to extrapolate soil
 337 water extraction patterns beyond 1 m, we estimated that by the end of the dry period, ~ 2.4 mm day⁻¹ of
 338 soil water was extracted from the top 2 m (Figure 5; Table 3).

339 *Fine root biomass distribution and soil water extraction*

340 Fine root biomass distribution measured for the top 235 cm of soil averaged 1.19 kg m⁻³ and ranged
 341 from 0.97 kg m⁻³ and 1.37 kg m⁻³ by soil core location. Fine root biomass distribution declined
 342 exponentially with depth, with 45% of root biomass (range 29-60%) in the upper 5 cm. Despite a decent
 343 exponential curve fit of biomass to depth using the Gale and Grigal (1987) model ($\beta = 0.8$, $R^2 = 0.92$),
 344 the cumulative root fraction between 20-50 cm was overestimated. Therefore, we tested a more complex
 345 yield-density model ($Y = d \times (a + b \times d^c)^{-1/c}$); where Y=root fraction and d=depth (Bleasdale and Nelder,
 346 1960), which provided a better fit to the data ($R^2 = 0.90$; $a = 1.5024$, $b = 0.9859$, $c = 0.8520$). Using the
 347 Bleasdale model, we fitted fine root biomass data to the depth of 235 cm (Figure 6). By integration, we
 348 found that 90% of the fine root biomass was distributed in the top 22 cm, 95% in the top 45 cm, and only
 349 ~4% between 45 and 150 cm soil depth. Moreover, we found a significant relationship between fine root
 350 biomass and soil water extraction; fine root biomass explained 59% of the variation of vertical soil water
 351 extraction (Figure 7); Michaelis-Menten kinetics model: $V_{\max}=0.25$, $K_m=0.00042$, $R^2=0.59$).

352 *Plot-level transpiration and soil water extraction*

353 The relationship between measured SA and DBH in this study was used to improve the allometric
 354 equation of Aparecido et al. (2019) (Figure S1). SA also had a strong positive linear relationship with
 355 tree T rate during the dry period (Figure 8; $R^2 = 0.91$). By application of these relationships across trees
 356 within a plot, plot level basal area could be used to derive plot level T rates (Figure 9), where increasing
 357 basal area explained 64% of the increase in plot T. Actual water use based on measured sap flow for the
 358 single dominant tree in each plot (equation 3), scaled to projected canopy ground area (Table 1), was 6-
 359 28% of the scaled allometric estimates of plot level water use based on the allometric scaling
 360 relationship between DBH and SF for all trees within the 5 m radius plot (Table 4). Greater daily water
 361 use per unit ground area of the sap flow trees resulted in a reduction in whole plot level T ($R^2 = 0.59$;
 362 Figure S3). Plot level tree T rates were significantly greater than measured water extraction from the
 363 upper 1 m of the soil profile; however, projected water extraction from the upper 2 m profile was
 364 equivalent to plot level T (Figure 10).

365 **Discussion**

366
 367 In this study, we linked tree water use to soil water availability and extraction patterns, root biomass
 368 distribution, and tree allometry to better understand drought-driven shifts in depth of water uptake. Even

369 so, the hyperdiversity within tropical forests can confound simple allometric scaling of water extraction
370 patterns due to species-specific variation in hydraulic strategies, as well as spatial patterns of tree
371 distribution and soil water extraction. Adequate consideration of the range of spatio-temporal responses
372 of stand level transpiration to drought can provide a framework for projecting water use based on
373 measured ecosystem traits, including soil properties, demographics, size, and dynamics of hydraulic
374 sensitivity and resistance, including via deeper water extraction, phenology, capacitance or hydraulic
375 redistribution. Even with such complexity, our results provide key information on the species-specific
376 regulation of transpiration by dominant trees as water availability changes, and the simultaneous
377 dynamics of soil water extraction that can be used to inform mechanistic models that project tropical
378 forest responses to drought.

379 *Divergent hydraulic sensitivity to drying*

380 Our first objective was to assess water use for different co-occurring canopy species as atmospheric
381 demand increases but upper soil water declines. We found that some tree species increased transpiration
382 rates during the month-long drought, while others decreased transpiration rates. There was also
383 differential and dynamic radial patterns of sap flow during the dry period, likely due to differential depth
384 of root water extraction, and timing and magnitude of transpiration and capacitance use and refilling –
385 topics that are currently under active investigation. Results highlight divergent species-specific hydraulic
386 strategies. Specifically, increases in transpiration indicate that these individuals have sufficient water
387 supply to meet increased atmospheric demand. An important consideration to water demand and supply
388 trade-offs is tree size. Generally, we expect that taller trees that rise above the canopy experience greater
389 water use due to greater exposure (Kunert et al., 2017), and that larger diameter trees can have greater
390 internal water storage capacity to help fulfill that demand (Scholz et al., 2011). Indeed, we found that the
391 emergent *B. grandis*, which had the greatest height and diameter, also had the steepest rate of increase in
392 daily T during drought.

393 We found a positive relationship between tree size and water use across the entire range of sampled tree
394 diameters, similar to that reported in other tropical forest studies (e.g., Meinzer et al. 2001 (Panama),
395 Kunert et al. 2017 (Central Amazon)). However, at narrower diameter ranges, this relationship can break
396 down due to differences in sapwood depth and hydraulic strategy. For example, trees larger than 30 cm
397 diameter had a wide range of sapwood area which was not well linked to diameter (Fig S1) or tree water
398 use; e.g., despite have a 60% greater diameter, the total daily Q for *B. grandis* was just one third that of
399 the smaller *O. nigrescens*, a result of the much lower SA of *B. grandis*. Similarly, in another nearby
400 study at ZF2, there was no relationship between diameter and water use for trees > 40 cm (Kunert et al.
401 2017). In contrast, for canopy tree species in Panama, there was a tighter relationship between SA and
402 diameter, and deep sapwood was more prevalent for the larger trees (Meinzer et al. 2001). While broad
403 scaling patterns are evident, the higher resolution differences in relationships between diameter, SA and
404 Q suggest that other phenological, structural and physiological characteristics such as wood density,
405 xylem vessel size, stem hydraulic conductivity and capacitance are also important for determining plant
406 water use (e.g., Bucci et al. 2008, Santiago et al., 2018). Across 27 co-occurring canopy trees in Panama,
407 sap flux density declined dramatically with tree size, although larger trees often have greater SA , which
408 could offset the reduced rates and maintain high total tree water use (Meinzer, Goldstein and Andrade
409 2001).

410 Tree water use and xylem transport rates also depend on sapwood water storage, or capacitance, which
411 increases with SA and can vary with wood physical properties; e.g., declining with wood density
412 (Meinzer et al. 2003). Leveraging capacitance during dry periods requires continued access to soil water.

413 Thus, deeply rooted trees may maintain high transpiration rates during drought (Lee et al., 2005; Baker
414 et al., 2008) when buffered by diurnal use and refilling of stored water in stem, or in the upper roots and
415 soils via hydraulic redistribution. Indeed, the importance of stem water storage (e.g., Goldstein et al.
416 1998, Sholtz et al. 2008, Yan et al. 2020) and hydraulic redistribution has been shown to be a significant
417 component of diurnal and seasonal water use during dry periods (e.g., Lee et al. 2005, Neumann and
418 Cardon 2012). Because both processes would provide a buffer for net daily declines in upper soil water
419 availability, apparent upper soil water stress can be delayed.

420 Alternately, decrease in T indicate that these individuals are sensitive to the drying of near surface soils.
421 After *B. grandis*, the next four largest trees were co-dominant, with similar heights. Still, drought-
422 responses differed. There was an increase in T for two trees, but a decline for the other two. Moreover,
423 two of the three smallest trees had flat or declining rate of T. The species-specific sensitivity to drought
424 is likely related to their hydraulic strategy, including stomatal sensitivity to VPD, phenology or leaf loss,
425 capacitance or rooting depth and ability to extract soil water held at high tensions. Because we found
426 that even a week without precipitation was sufficient to reduce much of the plant available water near
427 the soil surface, 0 cm to 40 cm deep, we might expect that some shallowly rooted species tolerate the
428 low leaf water potentials necessary to continue to extract water and maintain or increase T during short
429 dry periods, while others that cannot tolerate low water potentials would decrease T. One of the smallest
430 trees, *Eschweilera romeu-cardosoi*, displayed large increases in T during the dry period. This species
431 could meet increased water demands if it either tolerates low leaf water potentials, is deeply rooted, or
432 alternately, has more extensive lateral rooting that may be able to access pockets of higher water content
433 spatially across the landscape. Root distributions are remarkably diverse, and in some cases can extend
434 long distances across the landscape to access resources where available; e.g., a neotropical fig (*Ficus*
435 *schultesii*) in a Peruvian floodplain was found to have a 102 m long lateral surface root (Silman and
436 Krisel 2006).

437 *The forest shifts to deeper soil water extraction as soil dries*

438 Our second objective was to track shifts in the depth of water extraction as soils dry. Yet the ability to
439 extract soil water at deeper depths is constrained by rooting depth. We found that fine root biomass was
440 greatest near the surface. In fact, field observations indicated a root mat at the surface (<2 cm depth)
441 intermixed with a minimal leaf litter layer. After that, root density declined rapidly with depth. These
442 results are not surprising and agree with most studies in Central Amazon. For example, Chauvel et al.
443 (1992) showed that root length was concentrated in the superficial soil horizons but then decreased
444 rapidly with depth; i.e., 70 km m⁻³ at 0-30 cm depth, while deeper layers (1-6 m) were just 3.5-6.5 km m⁻³.
445 Ferreira et al. (2002) showed that 74% to 93% of fine root biomass was found in the top 20 to 40 cm
446 respectively; and Noguchi et al. (2014) showed that 89% of the fine root biomass in the plateau was
447 concentrated in the first 20 cm, in agreement with our results. The higher concentration of biomass of
448 fine roots near the surface is likely due to the higher levels of organic matter, litter decomposition and
449 nutrient cycling found in these layers, in addition to the physical structure of the soil (lower density,
450 higher porosity, higher concentration of sand). Observations at a nearby site with minirhizotrons
451 reported root length production and mortality were also much greater in upper soils, and more sensitive
452 to precipitation events (Cordeiro et al. 2020). Since these soils are generally nutrient poor, primarily low
453 in phosphorus (Lugli et al. 2020; B. Newman, unpublished data), root distribution at the surface can
454 convey competitive advantage for interception of nutrients released from surface litter decomposition.

455
456 In addition, high root density at the surface would allow for rapid uptake of precipitation, which could
457 be important to alleviating drought stress during periods when the frequency or magnitude of

458 precipitation is limited. While we did not assess surface root water uptake, we projected an exponential
459 increase in uptake towards the surface. The importance of this finding is that, despite the high
460 concentration of fine roots near the surface, it is the deeper roots which will become critical for
461 sustaining plant function during extended dry periods.

462
463 We found that at the stand-level, the forest generally shifted to deeper soil water sources. For another
464 study at K34, Broedel et al. (2017) reported a significant increase in the depth of water extraction during
465 the evolution of a drought. This pattern has also been found in other forest types with seasonal dry
466 periods (Nepstad et al., 1994, Hodnett et al., 1995; da Rocha et al., 2004; Warren et al., 2005; Bruno et
467 al., 2006; Nepstad et al., 2007; Tomasella et al., 2008). Hodnett et al. (1995) showed only 80 mm of
468 water were available in the soil to plants between 2 to 3.6 m. Even so, these deep layers provide
469 additional volume of water to the forest during dry periods as a way to compensate for the higher
470 evaporative demand, reflections of low levels of precipitation, high air temperatures and VPD, and low
471 air and soil humidity. Our data demonstrate that at the plot-level, there was an increase in total water
472 extraction and in water extraction with soil depth.

473
474 Soil water availability has been shown to be limited for the oxisols of the Central Amazon, with only
475 ~18% availability of total water between field capacity and the permanent wilting point in the upper 1 m
476 (Ferreira et al. 2002). Given the high clay content present at our site (Corrêa, 1984; Chauvel et al., 1992,
477 Marques et al., 2004), we would expect that in an extended dry period, root extraction exhausts the soil
478 water pool of the top 1 m and deeper soil water reserves must be tapped to sustain transpiration. If
479 deeper soil water is not available because soil is dry or there is a lack of roots, transpiration must
480 decline. In the more seasonal eastern Amazon, tree water use was reduced after a 21-day dry period
481 characterized by low soil moisture and high VPD, indicating a lack of water extraction from deeper
482 depths (Brum et al., 2018). At our site, upper soil water content declined substantially during the month-
483 long dry period, likely reaching the point where water was no longer available for plant uptake. For
484 example, at 15 cm depth (Figure 2B), water content declined from ~43% to 38% by the end of the
485 drought. Earlier work in a nearby plateau that modeled van Genuchten soil water release parameters
486 indicated water content at the wilting point (1500 kPa) was ~37% for the 10-20 cm layer (Ferreira et al.
487 2002), suggesting a substantial loss of water available for extraction. In our study, the lack of water
488 availability in the upper layers toward the end of the dry period illustrates the necessity of progressively
489 deeper water extraction to fulfill the transpirational demand of the trees. Since we observed divergent
490 trends in T rates during dry conditions, we expect that species which were heavy water users—increased
491 rate of T and a high daily T—were important in driving the shifted to greater plant-water-uptake depth.

492 *Discrepancy between stand level T and soil water extraction*

493 Our last objective was to predict T based on tree size, stand basal area, and soil water extraction in the
494 top 1 m. Specifically, we attempted to use allometric equations to scale tree size into stand-scale T and
495 then compared to total soil water extraction. There are several reasons that could lead to a discrepancy
496 between these methods. One reason is related to the assumptions we make to estimate stand-level T.
497 Essentially, we are asking, can we use diameter to estimate T? This question has previously been posed
498 by others. For example, Meinzer et al. (2001) found that diameter alone accounted for more than 90% of
499 the variation in both maximum and total daily sap flux density. Still, this study was conducted in
500 seasonally dry tropical forest, and unlike our study, is based on sap flux density measurements of the
501 outer 2 cm of sapwood, without accounting for radial variation which could lead to underestimations of
502 T (Moore et al., 2020). Other research has shown that stand-level, time-averaged scaling overlooks

503 species-level differences and fluctuation in environmental conditions (Anderson-Teixeira et al., 2015).
504 This is supported by species-specific differences in T rate, and hence the need for outlier detection when
505 performing allometric relationships between DBH, SAP, and T. That is, if we were to integrate over
506 different species, a longer timeframe, or contrasting environmental conditions, we would expect our
507 allometric relationships to change.

508
509 Another reason for the discrepancy between scaling methods is that there are inherent difference
510 between T estimated via sap flux sensors vs. estimated water extraction patterns in the top 1 m of soil.
511 Practically speaking, the point at which these water fluxes are measured and how measurements are
512 scaled is different. Measurements of tree water use via sap flux density will be skewed according to
513 wood physical properties and stem water content (Vergeynst et al., 2014), sensors placement in inactive
514 xylem (Clearwater et al., 1999), the accuracy of sapwood area estimates (Kumagai et al., 2005), and the
515 spatial and radial variations within the xylem (Tseng et al., 2017). Scaling thermal dissipation probe
516 voltage output to sap flux density also relies on an accurate calibration equation, which is not easily or
517 often measured, thus leading to potential bias in scaling using the standard equation (e.g., Bush et al.
518 2010). Moreover, sap flux-based estimates at the tree-level integrate across the soil depths from which
519 water is accessed. Measurements of soil water extraction, on the other hand, are limited to the depths at
520 which soil water is measured. Although we aimed to overcome some depth limitations by extrapolating
521 soil water extraction patterns to 2+ m depth, tree water access at even greater depths is likely, given the
522 presences of some roots (e.g., Negrón-Juárez et al. 2020), albeit at very low densities, and the necessity
523 for access to free water. Since stand-level T estimates were consistently greater than soil water
524 extraction estimates, and since we have seen a general shift towards deeper soil water during the dry
525 period, it is likely that soil water extraction extended beyond the 2 m depth during the study period, and
526 would certainly be deeper than 2 m under a more extended drought.

527 *Conclusions*

528 Our results provide field-based empirical evidence for a dependence on deep soil water sourcing due to
529 drought-driven shifts in tree water use in Central Amazon. Such findings are imperative given the
530 sensitivity of tropical forests to changes in climatic conditions and considering that in the past the humid
531 tropics have only experienced extreme water stress periodically, a pattern that is likely to change in the
532 future. Here we show that even a month of drought is sufficient to warrant a transpiration response. We
533 found that differential transpiration patterns for co-occurring canopy species, the major water users
534 contributing to stand-level signals, reflects divergent hydraulic strategies. And that even though most of
535 the tree root biomass is found near the soil surface, it is an increased dependence on deep soil beyond
536 the top 1 m or more that sustained transpiration for some species, and more generally, at the forest stand-
537 level. Moreover, discrepancies between sap-flux based allometric estimates of T and total soil water
538 extraction highlights challenges when scaling tree-based water use to stand-level estimates of ecosystem
539 water use at higher spatial scales, and thus provides impetus for a holistic assessment of contributing
540 soil, tree and environmental components in a modeling framework. Understanding how different species
541 respond to and cope with drought and quantifying this difference in terms of transpiration fluxes is
542 critical as a first step to upscaling forest dynamics and understanding validity of model representation
543 and community-scale generalizations. We expect that these findings will inform and help better
544 constrain mechanistic Earth Systems Models that are used to project functional responses of tropical
545 forests to drought.

546

547 **Author Contributions**

548 JW planned and designed the experiments. GS, BG, VM and JW performed the experiments. GS, CW,
 549 BG, VM and JW analyzed the data. GS, CW, BG, and JW wrote the manuscript. All authors contributed
 550 to fieldwork, analysis or improved the manuscript.

551 **Funding**

552 This material is based upon work supported as part of the Next Generation Ecosystem Experiments-
 553 Tropics (NGEE-Tropics) funded by the U.S. Department of Energy, Office of Science, Office of
 554 Biological and Environmental Research through contract No. DE-AC02-05CH11231 to LBNL, as part
 555 of DOE's Terrestrial Ecosystem Science Program. Additional funding for this research was provided by
 556 the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).
 557

558 **Acknowledgements**

559 The authors are thankful for the logistical and scientific support provided by the Laboratório de Manejo
 560 Florestal (LMF) and the Large-Scale Biosphere-Atmosphere Program (LBA) at the National Institute of
 561 Amazonian Research (INPA). We appreciate discussions with LBA hydrologist Dr. Sávio Ferreira and
 562 his team, and the meteorological data provided by the scientific manager of LBA, Dr. Alessandro C.
 563 Araújo.

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760 **Data Availability Statement**

761 The datasets generated for this study can be found in the NGEE-Tropics Data Archive and can be made
 762 available upon request.

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