Differential water-use strategies in co-occurring pioneers and late-successional tree species in secondary tropical montane forests of Eastern Himalaya

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Cover Letter to the Editor

21st January 2022

Dear Editor,

We are pleased to submit an original research article entitled “**Differential water-use strategies in cooccurring pioneers and late-successional tree species in secondary tropical montane forests of Eastern Himalaya**” for consideration for publication in the journal *Trees*.

The manuscript focuses on the plant-water relations in hitherto unstudied tropical montane forests (TMFs) of Eastern Himalaya, one of the 30 global biodiversity hotspots and global 200 ecoregions of importance. In this manuscript, using sap flow probes and the soil-plant-atmosphere-continuum (SPAC) framework, we present first detailed insights into the drivers of the variability in plant-water relations of cooccurring pioneers and late-successional species in a secondary Eastern Himalayan TMF. We hypothesized that the plant-water use by the pioneer species will be high but equally likely to be affected by environmental extremes, whereas late-successional species will have relatively stable water-use patterns. Our study site is **the wettest (mean annual precipitation = 4500 mm yr⁻¹) high-elevation (> 2000 meters) site in the world, where direct sap flow measurements have been carried out so far**. Thus, we also predicted that, due to high moisture availability, the ecosystem productivity is likely to be energy limited. We report one of the highest daily stand transpirations (5.3 mm) from among tropical montane or lowland forests, along with significant nocturnal transpiration, which is seen as an adaption to the dominantly afternoon-late-night summer rainfall in Eastern Himalaya. The drivers of transpiration shifted from energy (sunlight) in winters to atmospheric moisture availability (Vapour pressure deficit) in summers, whereas the differential access to solar radiation, a characteristic of the forest canopy in secondary forests, induced significant radial and azimuthal variability in sap flow. We postulate that the shallow-rooted pioneers are more responsive to environmental extremes and soil moisture fluctuations than the deep-rooted late-successional species. Thus, these regenerating secondary TMFs are highly susceptible to the negative impacts of the predicted warming and decline in winter precipitation.

We truly believe *Trees* will be an outstanding forum to share our work as the work **provides first mechanistic insights into the tree ecophysiological processes driving plant-water use and tree-environment interactions among different functional groups from the Eastern Himalaya**. The study will contribute to the scarce literature on plant-water relations from TMFs globally, and Himalaya particularly, and thus will be of great interest to many readers of your journal. More importantly, being the first report from the Eastern Himalaya, the study will interest the general public, media, policymakers, and governments in **highlighting the vulnerabilities of regenerating secondary forests to climate change impacts**.

36 The submitted manuscript entails original work and has not been published or submitted anywhere
37 else. We do not have any conflicts of interest to disclose.

38

39 Thank you for your consideration of this manuscript.

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44

45 **Differential water-use strategies in co-occurring pioneers and late-successional tree species in**
46 **secondary tropical montane forests of Eastern Himalaya**

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64 **Abstract**

65 Plant-water relations in secondary tropical montane forests (TMFs) are driven by complex interactions
66 between environmental conditions, species composition, and forest structure. We investigated the
67 differential water-use strategies of cooccurring pioneers and late-successional tree species in a secondary
68 TMF of Eastern Himalaya, India. It is the wettest (mean annual precipitation = 4500 mm yr⁻¹) high-
69 elevation (> 2000 m) site in the world. The observed maximum daily stand transpiration (5.3 mm) is
70 highest among other tropical montane or lowland forests. Although energy-limited, increased moisture
71 availability allowed the observed sap flux densities from the studied species, *Symplocos racemosa*, *Eurya*
72 *acuminata*, and *Castanopsis racemosa*, to be 3-9 times higher than their conspecifics from relatively drier
73 TMFs. Interestingly, differential access to solar radiation, a characteristic of the forest canopy in secondary
74 forests, induced significant radial and azimuthal variability in sap flow. Solar radiation was the key driver
75 of transpiration in energy-limited winters and Vapour pressure deficit in energy-abundant summers.
76 Nocturnal (1800-0500 h) transpiration was significant (13.8 %) part of daily T and was dominated by pre-
77 dawn flux. Shallow-rooted pioneers, *S. racemosa* and *E. acuminata*, exhibited strong midday depression in
78 sap flow in response to environmental extremes and soil moisture fluctuations, whereas the deep-rooted
79 late-successional *C. hystrix* transpired unaffected. The complex interactions between different successional
80 groups for accessing changing energy and moisture conditions are highlighted for prioritized conservation
81 and management of these secondary forests in Eastern Himalaya.

82 **Keywords**

83 Sap flow, Transpiration, Tree Ecophysiology, Plant Water relations, Secondary Forests, Ecohydrology

84 **Key message**

85 First reports of contrasting and interactive water use strategies among co-occurring pioneers and late-
86 successional tree species with highest maximum daily stand transpiration (5.3 mm) reported from
87 secondary tropical Eastern Himalayan forests.

88

1. Introduction

In most terrestrial systems, the availability of energy (and light) and water are the primary drivers of water-use by vegetation (Schulze et al. 1987, Heimann and Reichstein 2008). Spatiotemporal variability in temperature, precipitation, and soil moisture exert significant controls on the distribution and composition of vegetation (Todd et al. 2010, Piedallu et al. 2013). Over the long term, vegetation adapts to the environmental conditions and biological competition through functional traits and strategies enhancing photosynthesis and water-use efficiency (Ackerly et al. 2000, Troch et al. 2009, Tang et al. 2014). In turn, vegetation also significantly alters the availability of water in their environment through transpiration and hydraulic redistribution (Neumann and Cardon 2012, Schlesinger and Jasechko 2014). Transpiration taps into subsurface moisture and releases it into the atmosphere altering local moisture balance (Federer 1973, Barros and Lang 2003). This see-saw interaction between vegetation and moisture availability is the focus of studies on the Soil-Plant-Atmosphere-Continuum (SPAC), an active area of research in the field of ecohydrology (Asbjornsen et al. 2011, Manzoni et al. 2013, Mencuccini et al. 2019). The SPAC framework is mainly focused on the process of transpiration, which is the movement of water from the soil to the atmosphere via plant, based on a gradient of total water potential. It is driven by environmental variables like Vapour Pressure Deficit (VPD), an index of atmospheric dryness, light and soil moisture availability, and ecophysiological traits controlling plant water-use (Hetherington and Woodward 2003, Asbjornsen et al. 2011, Manzoni et al. 2013). These ecophysiological traits, such as wood anatomy, rooting depth, stomatal density, sapwood density, have evolved through competition and adaptation by co-occurring species belonging to different functional groups, and are expressed as inter-specific variability (between individuals of different species) (Phillips et al. 2010, Hernandez-Santana et al. 2015). The intra-specific (within individuals of the same species) variations manifests as radial and azimuthal variability in sap flow, and are influenced by growth stages, size, and individual responses to the microclimate (Fiora and Cescatti 2006, Berdanier et al. 2016, Berry et al. 2018). Such species-based understanding is important while scaling transpiration to individual and stand-levels, which requires using appropriate scalars, including biometric scalars like sapwood area, leaf area index (LAI), basal area, and tree height (Hatton et al. 1995, Barbour et al. 2005, Mackay et al. 2010). Failure to incorporate the intra and inter-specific variability, along with logistical limitations of measuring sap flow in a limited number of tree individuals, can

117 contribute to large biases in estimating stand transpiration, especially in bio-diverse secondary tropical
118 montane forests (TMFs) (Čermák et al. 2004, Forrester 2015, Hernandez-Santana et al. 2015).

119 Ecohydrological studies describing mechanistic linkages micro-environment, ecophysiological
120 traits, and transpiration in TMFs are largely restricted to the tropical Andes and South-East Asia with very
121 little research coming from Himalaya (Bruijnzeel, Mulligan, & Scatena, 2011; Buytaert, Celleri, Willems,
122 Bièvre, & Wyseure, 2006; Céleri & Feyen, 2009). Studies on plant-water relations from the Himalaya have
123 focused on inter-specific patterns in leaf water potential with environmental gradients, most coming from
124 the drier Western Himalaya (Poudyal et al., 2004; Singh et al., 2006; Zobel & Garkoti, 2001). Direct
125 measurements of whole-tree transpiration using sap-flow methods are rare, and here Ghimire et al. (2014)
126 stand out for comparing variability in transpiration rates between needle-leaved Chir pine (*Pinus*
127 *roxburghii*) and broad-leaved Oak forests in Central Himalaya. Previous studies have highlighted the
128 crucial role of seasonal soil moisture fluctuations on phenology and growth cycles in broad-leaved trees
129 (Chand, Poudyal, & Jha, 2017; Singh, Tewari, Singh, & Pathak, 2000; Tewari, Bhatt, & Mittal, 2016).
130 Similarly, research indicates differential growth rates between dry and wet sites and across elevation
131 gradients, again with soil moisture being the key limiting variable (Poudyal et al. 2004b, Shrestha et al.
132 2015). Others have explored the variability in their ecophysiological responses to seasonal moisture deficit
133 across elevation, species range and canopy structure (Zobel et al. 2001, Singh, Zobel, Garkoti, et al. 2006,
134 Tewari et al. 2018). They have also pointed that a majority of the broad-leaved TMFs in the Himalaya are
135 secondary in nature due to the long history of human forest use (Ramakrishnan and Kushwaha 2001,
136 Kanade and John 2018). Secondary TMFs differ significantly from their primary counterparts in terms of
137 species composition, stand structure, and ecophysiological functioning (Ramakrishnan and Kushwaha
138 2001, Nogueira et al. 2004). Globally secondary forests form a significant carbon sink and play a major
139 role in regional ecohydrology (Giambelluca 2002, Wohl et al. 2012, Brown et al. 2019). However, few
140 studies have explored the ecohydrological dynamics of bio-diverse secondary tropical montane forests in
141 Eastern Himalaya, where vegetation-driven evapotranspiration can range from 30% - 47% of the total water
142 budget (Acharya et al. 2011, Patle et al. 2020). The region is threatened by the prediction of a high rate of
143 warming (+5°C) and precipitation changes (+40%) under climate change (Kulkarni et al. 2013).

144 Sikkim, representing the Eastern Himalayan eco-climatic zone, is characterized by steep
145 topography, complex geomorphology, high rainfall, and diverse ecosystems (Bookhagen and Burbank
146 2010, Tambe et al. 2011). Broad-leaved forests (800 – 2800 masl) form the most dominant vegetation type
147 in Sikkim (Tambe et al. 2011). A third of these are secondary forests modified by decades of anthropogenic
148 pressures and remain understudied (Kanade and John 2018). They provide sanctuary to the principal water
149 resources, the springs and streams, and understanding their plant-water relations is critical to the regional
150 water and ecological security (Tambe et al. 2012). Plant-water relations have not been studied in the wet
151 secondary TMFs of Eastern Himalaya using direct whole-tree methods. To address the knowledge gap, we
152 use the SPAC framework to understand the relative influences of the wet tropical environment and
153 secondary forest structure on plant-water relations in an East-Himalayan broad-leaved evergreen secondary
154 TMF. Specifically, we address two main questions: (a) What are the environmental and ecophysiological
155 drivers of water-use in key broad-leaved evergreen tree species under wet tropical Eastern Himalayan eco-
156 climate? and (b) How the plant-water strategies differ between co-occurring pioneers and late-successional
157 species in a secondary forest structure? The study is conducted in an early successional secondary forest
158 stand which is representative of the East Himalayan broad-leaved evergreen wet montane forest
159 classification and is dominated by a mix of pioneers and late-successional emergent species. The site is
160 unique in being the wettest (mean annual precipitation (MAP) ~ 4500 mm yr⁻¹) high-elevation (> 2000
161 masl) site in the world, where direct transpiration measurements have been carried out so far (McJannet et
162 al. 2007, Bruijnzeel et al. 2011). Being one of the 30 global biodiversity hotspots and global 200 ecoregions
163 of importance, the studied broad-leaved forests in Eastern Himalaya are also the most species-rich TMFs in
164 the world (Brooks et al. 2006, Bajracharya et al. 2010).

165

166 **2. Materials and methods**

167 **2.1. Study site and forest stand description**

168 The study was carried out in a micro-watershed (27.35° N, 88.56° E) in the Fambong-Lho
169 Wildlife sanctuary (FWS), Sikkim, which is part of the Teesta River basin (Figure 1). The total watershed
170 area was 1.6 hectares and elevation ranged from 2150 - 2400 meters above sea level (masl). The mean

171 annual precipitation between the years 2013-2016 was 4649 ± 120 mm and the mean annual daily
 172 temperature ranged from -2°C to 24°C . The year is divided into three distinct seasons: Summer (MAM)
 173 characterized by warm days, cloudy afternoons, significant pre-monsoon precipitation, and high
 174 evapotranspiration; Monsoon (JJASO) with concentrated precipitation, high humidity, and low
 175 evapotranspiration; and Winter (NDJF) with bright days, cold nights, occasional snowfall events and
 176 moderate evapotranspiration (Pandey et al. 2016, Kumar et al. 2021). The forest sloped at 10° - 35° ,
 177 predominantly facing the north-east direction, and the soil was well-drained sandy-loam with an average
 178 soil depth of 70 cm. The forest stand represents the East Himalayan broad-leaved wet montane forests
 179 (Sudhakar et al. 2008, Kanade and John 2018) characterized by (a) the dominance of broad-leaved
 180 evergreen species and (b) sub-tropical montane climate with high precipitation and strong diurnal and
 181 seasonal temperature gradients. The vegetation data were derived from five 0.1 ha (100 m X 10 m)
 182 vegetation survey plots laid in FWS as part of another study (Bhutia et al. 2019). In each plot, all
 183 individuals above 30 cm circumference at breast height were enumerated and voucher samples were
 184 collected for identification. The composition and local history mark the stand as early successional
 185 secondary forest regenerating from past anthropogenic pressures (Sudhakar et al. 2008, Kanade and John
 186 2018). The top three dominant species in terms of tree density and basal area, *Symplocos racemosa*, *Eurya*
 187 *acuminata* and *Castanopsis hystrix*, were chosen for sap flow instrumentation (see supplementary data
 188 Figure S1). Out of these, the first two, *S. racemosa* and *E. acuminata*, are pioneers while the *C. hystrix* is a
 189 late-successional species.

190

191 Figure 1: (a) Digital elevation model (DEM) map of Sikkim showing; (b) the elevation profile of the
 192 Fambong-Lho wildlife sanctuary (FWS) and (c) delineated catchment maps of FMBL stream in FWS. The
 193 maps are prepared in QGIS (QGIS.org 2021) using the ASTERGDEM 003 (elevation in meters).

194

195 In the forest stand, the pioneer tree species dominate the short-statured canopy. The older and large-girthed
 196 remnant individuals of the Fagaceae family such as *C. hystrix* standing out as emergent. Table 1

summarises the information on rooting depth, phenology, and other ecophysiological characteristics of the three species collated from available literature and personal observations (Ohsawa et al. 1986, Suzuki et al. 1991, Sundriyal and Sharma 1996, 2003, Chettri et al. 2002, Sharma et al. 2011, Li et al. 2013).

200

Table 1. Life-forms and ecophysiological characteristics of the three species used for sap flow measurements.

203

2.2. Sap flux measurements

Sap flux was measured in a total of 13 individuals of the three dominant species using Granier's thermal dissipation method-based probes (TDPs) (Table 2) (Granier 1987, Lu et al. 2004). The sample size of 13 trees (5 trees each of *S. racemosa* and *E. acuminata*, and 3 trees of *C. hystrix*) was at the higher end of the average number of trees sampled in sap flow studies globally (Mackay et al. 2010, Asbjornsen et al. 2011). TDPs are known to perform well in cold and low-flow conditions (Lu et al. 2004, Chan and Bowling 2017). The probes were manufactured locally based on suitable modifications to the original design with only the top one cm measuring the sap flux (for details see Phillips et al. 1996, James et al. 2002, Harmon 2009, Davis et al. 2012). The choice of radial and azimuthal installation sites on a tree was carefully done to optimize number of sensors and xylem variability (Guyot et al. 2015). We installed radial probes (1-5 cm in length) spirally at one cm incremental depth from the cambium in one tree per species. The replicate trees were fitted with two 2-cm length probes installed in north and south azimuthal aspects (Shinohara et al. 2013, Komatsu et al. 2016). The length of sapwood was measured using wood cores extracted using an increment borer. *C. hystrix* showed distinct heartwood formation and only the outer xylem (4-5 cm) was functional. No heartwood was detected in *S. racemosa* and *E. acuminata* and the entire xylem was assumed functional, a characteristic of diffuse-porous species (Berdanier et al. 2016). The probe signals (in millivolts) were recorded and converted to temperature difference (ΔT in $^{\circ}\text{C}$) between the heater and reference sensors and stored in a multi-channel datalogger (DL2e, Delta-T, UK). Sap flux density (J in cm^3

cm² hr⁻¹) was computed using Granier's empirical equation (equation 1) and maximum temperature difference ($\Delta T_{\max}$) was calculated daily (for details see Granier 1987, Lu et al. 2004).

$$J = 119 * 10^{-6} * 3600 * \left(\frac{(\Delta T_{\max} - \Delta T)}{\Delta T} \right)^{1.231} \quad (1)$$

The period of data collection was from November 2013 to May 2014. The first two weeks of data were ignored to avoid sap flux underestimation due to installation wounds (Wiedemann et al. 2016). Due to very wet conditions, especially in the summer, it was difficult to maintain the field instrumentation for a long duration and data gaps were inevitable (see supplementary data Figure S2 for time-series plots of the data used in the analysis). After due quality checks, a total of 114 days of sap flow data across all species was used for the final analysis (species-wise break-up provided in Table 2). The data processing, analysis, and visualization were done in R (version 3.6.0) (R Core Team 2021) using RStudio (RStudio Team 2021).

Table 2. Biometric details ($\pm$ standard deviation) along with the total number of data days and number of radial probes installed for the three species.

2.3. Environmental and hydrological measurements

Soil water potential was recorded at 10 cm incremental depths from the topsoil using granular matrix-based (watermark) sensors (Virtual Electronics, Roorkee) and converted to volumetric water content using the site-specific van Genuchten water retention curve (Schaap et al. 2001, Gribovszki 2018). Total soil moisture (S in mm h⁻¹) was computed for the topsoil (0-30 cm depth) using the trapezoidal method (Nachabe et al. 2005). S was smoothened using a 3-step moving-average window to gap-fill stray missing values. In-canopy air temperature and relative humidity were recorded (iButton Hygrochrons, Maxim Int., USA). Air temperature ($^{\circ}$ C), relative humidity (R_h in %), wind speed (u in m s⁻¹), and incoming short-wave radiation (R_s in kW m⁻²) were recorded using an automatic weather station (AWS) (Vantage-pro Davis Net, USA). Vapour pressure deficit (VPD, kPa) was averaged for the separate VPD values calculated from the hourly air temperature and relative humidity data observed by the Hygrochrons and AWS. Precipitation (P

in mm h⁻¹) was recorded using an automated tipping-bucket rain gauge. Reference evapotranspiration (E_T) was computed based on FAO's Penman-Monteith method (FAO56PM, for detailed steps please see Allen et al. 1998), which was reported to be the suitable method for estimating E_T at the nearby Gangtok in Sikkim (Pandey et al. 2016). Leaf area index (LAI) was extracted for the site from MCD15A3Hv006 level-4 product (4-day temporal and 500 m pixel resolutions) from the Moderate Resolution Imaging Spectroradiometer (MODIS) (Myneni et al. 2015).

253

254 **3. Data analysis**

255 **3.1. Scaling from the probe to stand transpiration**

256 **3.1.1. Scaling from sap flux density to whole-tree sap flow**

We used a combination of the zero-averaged technique and weighted mean method to estimate whole-tree sap flow (V_{rad} in kg hr⁻¹) in radial trees (for details see Hatton et al. 1990, Pausch et al. 2000). Additionally, sap flow (V_{rad.2cm} in kg hr⁻¹) in the radial tree was also estimated assuming homogenous radial flow from J at 2nd cm depth (J_{2cm}) and total sapwood area (A_{total}) in the tree (equation 2).

$$261 \quad V_{\text{rad.2cm}} = J_{2\text{cm}} * A_{\text{total}} * 10^{-3} \quad (2)$$

V_{rad.2cm} showed significant overestimation (15 %) in reference to V_{rad} suggesting the use of an appropriate scaling mechanism to incorporate the diurnal variability in radial patterns.

Studies have used simple linear regression models (LRMs) between integrated whole-tree sap flow (V_{rad}) and sap flow in outer xylem for the trees with only outermost sensors (V_{rad.2cm}) (Paudel et al. 2013, Berdanier et al. 2016). However, considering the diurnal variability in their relationships, we chose to develop linear regression models without intercept for each hour of the day (see supplementary data Table S1). The slopes (m) of the LRMs each hour were multiplied with the average of sap flux density at the north (J_{north}) and the south-facing (J_{south}) probes and the total sapwood area (A_{total}) to estimate sap flow (V_{rep.LM} in kg hr⁻¹) in the replicate trees (V_{rep.LM} in kg hr⁻¹) using equation 3 (Paudel et al. 2013, Berdanier et al. 2016).

$$V_{\text{rep.LM}} = \left(\frac{J_{\text{north}} + J_{\text{south}}}{2} \right) * A_{\text{total}} * m * 10^{-3} \quad (3)$$

273

274 3.1.2. *Scaling from whole-tree sap flow to stand transpiration*

275 A five-step approach was adopted to scale sap flow (V in kg hr^{-1}) from the instrumented trees to
 276 the stand-level. First, a non-linear least squared (NLS) regression model (intercept = 0.112, power
 277 coefficient = 0.857, $P < 0.001$) was fitted between tree diameter (DBH in m) and sapwood area (A_{total} in
 278 m^2) of the 13 trees (see supplementary data Figure S3). The NLS regression model coefficients were used
 279 to compute total sapwood area (A_{total}) from DBH for each tree (above 10 cm DBH) sampled in the
 280 vegetation plots in the next step. Third, the instrumented trees were categorized into four DBH classes <
 281 0.15 m, 0.15-0.19 m, 0.20-0.24 m, and > 0.25 m (see supplementary data Figure S4a). The average sap flux
 282 density per class (J_{avg}) was computed by normalizing the V of each instrumented tree by its A_{total} and
 283 averaging for each class. Fourth, all trees above 10 cm DBH sampled in the vegetation plots were
 284 categorized into the above-mentioned DBH classes (see supplementary data Figure S4b). Whole-tree sap
 285 flow (V) was estimated for each tree in the forest stand by multiplying the corresponding J_{avg} of the
 286 diameter class with its A_{total} . Fifth, stand transpiration (T in mm h^{-1}) was computed by aggregating V for all
 287 trees in the four plots and dividing it by the total plot area. Gap-filling of the missing data for sap flow and
 288 environmental variables was consciously avoided due to the strong variability in the existing raw data and
 289 mixed results from the modeling exercise detailed later in the manuscript.

290

291 3.1.3. *Biases in the estimation of tree sap flow and stand transpiration*

292 We also estimated biases in whole-tree sap flow for replicate trees using the conventional scaling
 293 based on assumptions of uniform radial profile (Kume et al. 2012, Shinohara et al. 2013). The radially
 294 uniform sap flow estimate ($V_{\text{rep.CM}}$ in kg hr^{-1}) was developed using the two diametrically opposite 2-cm
 295 probes only without any hourly slope values, thereby ignoring the radial variability (equation 4). Similarly,

whole-tree sap flow ignoring azimuthal variability ($V_{rep,N}$ in $kg\ hr^{-1}$) was estimated $V_{rep,N}$ was estimated using the north-facing probe (J_{north}) only without any radial scalars (equation 5). Both the estimates were compared with whole-tree sap flow estimated by incorporating radial variability ($V_{rep,LM}$) as the reference, which was estimated using the hourly slopes of LRMs in equation 3 (Kume et al. 2012, Shinohara et al. 2013).

$$V_{rep,CM} = \left(\frac{J_{north} + J_{south}}{2} \right) * A_{total} * 10^{-3} \quad (4)$$

$$V_{rep,N} = J_{north} * A_{total} * 10^{-3} \quad (5)$$

Both $V_{rep,CM}$, $V_{rep,N}$, and $V_{rep,LM}$ were scaled to stand transpiration using the above-mentioned procedure and stand-level biases were estimated.

3.1.4. *Intra and interspecific variability in sap flow*

Four indices were chosen to visualize and quantify radial and azimuthal variabilities (Delzon et al. 2004, Fiora and Cescatti 2006, Shinohara et al. 2013):

(a) Daily maximum sap flux density (J_{max}) indicated regions of higher activity in the sapwood and was plotted against the depth from the cambium.

(b) The percentage contribution of the sapwood annuli at each depth to daily V was estimated as a product of the sapwood area of the annulus and the corresponding J .

(c) Hourly correction factors (C_h) was estimated for sunny days in trees with radial probes as the sum of hourly ratios of J at different depths in reference to J_{2cm} , normalized by the sapwood area of the annulus (A_i) over A_{total} (Delzon et al. 2004) (equation 6).

(d) Sap flow ratios (R_{NS}) were estimated as hourly ratios between J_{north} to J_{south} in replicate trees with azimuthal probes for all hours (Shinohara et al. 2013).

$$C_h = \sum_{i=1}^n \left(\frac{J_i}{J_{2cm}} \right) * \left(\frac{A_i}{A_{total}} \right) \quad (6)$$

Species-wise multiple linear regression models (MLRs) were fitted for the day (0600-1700 h) and night (1800-0500 h) periods to assess the relative roles of environmental variables R_s , VPD, and S in driving indices of radial (C_h) and azimuthal (R_{NS}) variability (Barbeta et al. 2012). Sap flow between 1800-0500 h was considered nocturnal (V_{night}) and its percentage contribution to daily V was estimated. Further, V_{night} was split into evening (1800-2300 h, $V_{evening}$) and pre-dawn (0000-0500 h, $V_{pre-dawn}$) components (Forster 2014). Species-wise MLRs using V_{night} as the response variable and VPD, S, and wind speed (u) as predictor variables were fitted to understand the environmental drivers of nocturnal sap flow (Barbeta et al. 2012). In the abovementioned MLRs, R_s , VPD, and S were centered on their respective daily means to facilitate the interpretation of the results. Diurnal patterns in sap flow of the three species and stand transpiration were visualized and assessed for variability across seasons.

329

3.2. *Environmental controls on transpiration under SPAC*

3.2.1. *Lag analysis between transpiration and SPAC variables*

Lag correlation analysis was used to compute seasonal lag between SPAC variables. The S time-series was de-trended to remove excessive noise (*stlplus* function, package *stlplus*) and the filtered diurnal signals (S_{diu}) were used (Moore et al. 2011, Gribovszki 2018). Hourly lag was computed (*ccf* function in R) for each day between the following combinations: R_s vs. T, VPD vs. T, and T vs. S_{diu} , and filtered for auto-correlation coefficients (ACF) $>= |\pm 0.4|$ (Komatsu et al. 2010, Moore et al. 2011).

337

3.2.2. *GLS linear regression model for transpiration*

The relative influences of predictor variables on the response variable were quantified using a combination of a temporal lag model and the Generalized least squares (GLS) regression model (*gl*s function, package *nlme*) with a suitable correlational structure. The Generalised least-squared (GLS) regression method estimates the maximum likelihood of the regression coefficients using generalized least-squares and is suitable for analyzing time-series data with auto-correlational structures (Pinheiro and Bates

2006, Krishnaswamy et al. 2012). Solar radiation (R_s , kW m^{-2}), Vapour pressure deficit (VPD, kPa), soil moisture (S , mm hr^{-1}), and Antecedent moisture index (M_a , mm hr^{-1}) were centered by subtracting the daily mean from the time-series and tested for collinearity. Contiguous subsets longer than 5 days and without any missing values were first tested for temporal lag between the driver-response variables using the cross-correlation function (*ccf* in R). If any significant lag ($\text{ACF} \geq |\pm 0.2|$) was observed, the driver variable was lagged by a suitable range of hours to develop multiple lagged time-series starting from zero lag time and a multiple linear regression model was fitted with the response variable. The procedure was repeated with each of the driver variables and the lagged time-series with the lowest significant lag ($P \leq 0.05$) was chosen to develop a reconstituted dataset. The GLS models used the predictors from the reconstituted data for subsequent analysis. The results of GLS models with correlations structures were compared with a similar GLS model without any autocorrelation structure using the Analysis of variance (ANOVA) test. The GLS models with the lowest Akaike information criterion (AIC), higher likelihood ratio, and significance were chosen for interpretations. The transpiration GLS model used T as the response variable and R_s , VPD, and S as predictor variables with second-order autoregressive moving average correlational structure (corARMA). The observed and predicted time-series of transpiration were compared using linear regression models and Gupta-Kling Efficiency (KGE) score to assess the model performances (Gupta and Kling 2011).

361

362 4. Results

363 4.1. Intra and interspecific comparisons of sap flux density and volumetric sap flow

364 The pioneer species, *S. racemosa* and *E. acuminata*, exhibited double rates of sap flux density (J) in comparison to *C. hystrix*, the late-successional species (Table 3). Whole-tree sap flow (V) increased linearly with total sapwood area across the species ($r^2 > 0.71$, $P < 0.001$). Therefore, *S. racemosa* and *E. acuminata*, with entire xylem conducting water, transpired at double rates of *C. hystrix* of comparable DBH, which had significant non-conducting heartwood. The peak sap flow in *S. racemosa* and *E. acuminata* occurred quite early in the day (0700-0800 h) whereas *C. hystrix* peaked around noon (1200 h). the Incidentally, small and medium-sized trees ($\text{DBH} < 0.2 \text{ m}$) contributed to 46 % of T , whereas large-

girthed trees (DBH > 0.25 m) contributed up to 40 %. Radial bias due to assumptions of homogenous flow along the xylem led to an overestimation of V in all three species. However, failure to account for azimuthal variability (azimuthal bias) caused significant underestimation of V in *C. hystrix* and *S. racemosa* but overestimation in *E. acuminata*. At the stand-level, failure to account for radial variability overestimated T, whereas azimuthal variability induced significant underestimation.

Table 3. Estimates of sap flux density (J), tree sap flow (V), tree-to-tree coefficient of variation in sap flow (COV) in the studied species and at stand-level. Percentage biases in sap flow estimation due to ignoring radial and azimuthal variability (standard deviation in parentheses) are presented across species and in stand transpiration.

4.2. Intraspecific variability in sap flow

4.2.1. Radial variability in sap flow

Radial patterns in $J_{\max}$ varied across the three species but remained consistent across the seasons. Both *S. racemosa* and *E. acuminata* exhibited concave curves in $J_{\max}$, with peaks at the outer and innermost xylem (Figure 2a). Correspondingly, the percentage contribution of each depth to daily V declined uniformly from the outermost xylem inwards for *S. racemosa* and *E. acuminata* (Figure 2b). Conversely, *C. hystrix* showed the highest $J_{\max}$ in the inner xylem at 4th cm depth from the cambium and its contribution to daily V was disproportionately higher (40 %). The importance of the inner xylem in water transport in *C. hystrix* is further corroborated by the highest wood moisture and lowest wood density at 4th cm depth (see supplementary data Figure S5). Overall, the three species, except *E. acuminata*, show an increase in mean daily J with wood moisture and a decline with wood density for a particular sapwood annulus ring (see supplementary data Figure S6). The relative contributions of sapwood rings to whole-tree sap flow remained similar for day and night across the species. Incidentally, the innermost probe at 5th cm depth in *C. hystrix* stopped showing any sap flux movement after January, which may be due to the loss of function

as the inner sapwood transitioned into non-functioning heartwood (Moore et al. 2010, Brodersen et al. 2019).

Figure 2. Radial variability in sap flow in the three species along the depth of xylem in (a) average daily maximum sap flux density ($J_{\max}$), and (b) percentage contribution of sap flow at different sapwood depths to daily whole-tree sap flow (V , kg hr^{-1}) (the error bars represent standard errors).

The three species displayed contrasting diurnal patterns in the radial correction factor (C_h) (Figure 3a). C_h values above and below one suggest underestimation and overestimation by the 2nd cm probe in reference to the rest of the xylem, respectively. In *S. racemosa* and *E. acuminata*, the 2nd cm probe underestimated sap flow in reference to the rest of the xylem ($C_h > 1$) in the evening-night period (1700-0300 h) and overestimated ($C_h < 1$) in the day (0400-1600 h). Contrastingly, in *C. hystrix*, the 2nd cm probe overestimated sap flow ($C_h > 1$) in night-morning (2300-0900 h) and overestimated ($C_h < 1$) in noon-evening (1000-2200 h) periods. On a closer look, the variability in C_h was driven by the higher sap flux density at outer xylem (1st cm depth) in *S. racemosa* and *E. acuminata*, and at inner xylem (4th cm depth) in *C. hystrix* to the rest of the xylem. The MLRs results suggested that daytime radial variability (C_h) was strongly predicted by R_s (negative slope) and S (positive slope) in *S. racemosa* ($r^2 = 0.43$, $P < 0.001$) and weakly predicted by R_s (negative slope) ($r^2 = 0.01$, $P < 0.15$) in *C. hystrix*, whereas none of the predictors were significant for *E. acuminata* ($r^2 = 0.01$, $P < 0.6$) (see supplementary data Table S2). Conversely, VPD was a strong negative predictor of night C_h in *E. acuminata* ($r^2 = 0.4$, $P < 0.001$) and a weak negative predictor in *S. racemosa* ($r^2 = 0.02$, $P < 0.2$) and *C. hystrix* ($r^2 = 0.001$, $P < 0.6$).

Figure 3. Variability in sap flow across the three species in (a) diurnal patterns in correction factor (C_h , unitless) used a proxy of radial variability, (b) diurnal patterns in sap flow ratios (R_{NS} , unitless) used as a proxy of azimuthal variability. The horizontal dotted lines mark the ideal value (1), and error bars represent standard errors.

422

423 *4.2.2. Azimuthal variability in sap flow*

424 Both *S. racemosa* and *E. acuminata* exhibited consistently high sap flow ratios (R_{NS}) throughout
 425 the day (Figure 3b). Interestingly, in *C. hystrix*, the northern probes dominated in the morning and the
 426 southern probes afternoon onwards. The MLRs predicting R_{NS} performed poorly ($r^2 \sim 0.03-0.18$) across the
 427 species (see supplementary data Table S3). However, R_s (positive slope) was a significant predictor of R_{NS}
 428 at average VPD and S across the three species ($P < 0.09$). Night-time azimuthal variability was better
 429 predicted by VPD ($P < 0.06$) and S ($P < 0.08$) in *S. racemosa*; and by VPD in *C. hystrix* ($P < 0.004$). S was
 430 a significant predictor of night R_{NS} in *E. acuminata* ($P < 0.04$).

431

432 *4.3. Interspecific variability in sap flow and environment*

433 *4.3.1. Diurnal patterns in sap flow and transpiration in relation to environment*

434 Both *S. racemosa* and *E. acuminata* showed low sap flow at high values of R_s and VPD (see
 435 supplementary data Figure S7). The heightened sensitivity to the environmental extremes manifested in
 436 bimodal peaks in diurnal sap flow with strong midday depression (V_{midday}) across the sampled trees (Figure
 437 4). The timing of V_{midday} coincided with peaks in VPD and R_s and troughs in S. Contrarily, *C. hystrix*
 438 maintained high V at extreme R_s and VPD with a unimodal peak. Minor signs of V_{midday} were seen in two
 439 out of the three trees in *C. hystrix*. Nocturnal sap flow (V_{night}), as a fraction of daily V, was highest in *E.*
 440 *acuminata* followed by *C. hystrix* and *S. racemosa* (see supplementary data Table S4).

441

442 Figure 4. Diurnal patterns of sap flow (V , kg hr^{-1}), Incoming short-wave radiation (R_s , kW m^{-2}), and
 443 Vapour pressure deficit (VPD, kPa) across the three species (values are normalized by their respective daily
 444 means for visual scaling and error bars represent standard errors).

445

446 *4.3.2. Nocturnal sap flow*

447 A significant proportion of V_{night} happened at pre-dawn in *S. racemosa*, whereas evening flux
 448 dominated in *E. acuminata* and *C. hystrix*. At the stand-level, nocturnal transpiration was a significant
 449 fraction of ($13.8 \pm 6\%$) of the daily T with a marginally higher proportion of evening than pre-dawn flux.
 450 Across the species, V_{night} was concentrated around low VPD (< 0.1 kPa), low wind velocity (< 0.5 m s⁻¹),
 451 and moderately saturated soil moisture conditions (see supplementary data Figure S8). The MLR models
 452 predicting V_{night} concurred with the observations (see supplementary data Table S5). S (negative slope) was
 453 a significant predictor of V_{night} in *E. acuminata* ($r^2 = 0.12$, $P < 0.05$) and VPD (negative slope) was a
 454 significant predictor for *C. hystrix* ($r^2 = 0.13$, $P < 0.009$). None of the predictors were significant for *S.*
 455 *racemosa* ($r^2 = 0.02$, $P > 0.5$).

456

457 *4.3.3. Seasonal changes in diurnal patterns of sap flow, transpiration, and environment*

458 Figure 5 depicts changes in diurnal patterns of SPAC variables from winter to summer as the
 459 growing season progressed. The winter (December-February) marked the dry season with bright but cold
 460 days, sub-zero night temperatures, low VPD, and declining soil moisture and streamflow. March onwards
 461 summer rains started, replenishing the soil moisture reserves and promoting leaf flush. The summers
 462 (March-May) saw increased day-length, abundant moisture, warmer temperatures, and higher plant
 463 productivity. Consequently, T also increased from winters to summer peaking in April. The seasonal
 464 pattern was corroborated by LAI and PET which peaked in April-May (see supplementary data Figure S9).

465 However, the transpiration rates varied between the species and across the seasons. Both *S.*
 466 *racemosa* and *E. acuminata* exhibited peak sap flow in December and March, whereas *C. hystrix* peaked in
 467 March-April. The overall variability in sap flux across species followed similar patterns. Radial variability
 468 in sap flux increased across the dry season for *S. racemosa* and *E. acuminata*, whereas the opposite trend
 469 was seen in *C. hystrix*. The fractional contribution of the outer xylem to daily V increased from December

to March for *E. acuminata* and *C. hystrix*, whereas the corresponding changes were marginal in *S. racemosa*. Azimuthal variability also increased from winter to summers for *S. racemosa* and *E. acuminata*, whereas in *C. hystrix* it was higher in January. Diurnally, the peak sap flow values increased with the growing season, except for *S. racemosa*, although the timing remained consistent across the species. The bimodal peaks in diurnal sap flow were seasonally consistent for *S. racemosa* and *E. acuminata*, with higher rates in the morning than afternoon. However, the weak $V_{\text{mid-day}}$ behaviour in *C. hystrix* was restricted to the relatively drier months and shifted to unimodal peaks from March onwards. Weak declining trends in V_{night} were observed from dry to wet season in all three species. The diurnal peaks in S_{diu} shifted from afternoon to evening with increasing amplitude from winter to summer. However, simple correlation tests between the SPAC variables yielded low correlations due to temporal lags between the variables.

Figure 5. Seasonal changes in diurnal patterns of SPAC variables from winters (December) to summers (May): (a) Incoming short-wave radiation (R_s), (b) Vapour Pressure Deficit (VPD), (c) S_{diu} is diurnal component of soil moisture, (d), (e) and (f) are the Volumetric sap flow rate (V) of *S. racemosa*, *E. acuminata*, and *C. hystrix*, respectively, and (g) Stand Transpiration (T). Each line represents monthly average values.

4.4. Environmental controls on transpiration under SPAC

4.4.1. Lag analysis between transpiration and SPAC variables

The cross-correlation analysis explored the shifting lags between SPAC variables across seasons (Figure 6). Positive (negative) autocorrelation coefficient (ACF) values signified that a high (low) value of the driver variable was followed by a high (low) value of the response variable after the corresponding lag-hours. T consistently lagged behind R_s and VPD by an average lag of 1-3 h with a strong positive correlation. However, on days with significant pre-dawn flux, T was ahead of R_s and VPD by an average of

3-5 h with strong positive correlations. However, the interactions between T and S_{diu} could be separated into two distinct periods: dry (December-February) and wet (March-May). In the dry period, initially, S_{diu} led T by 1-5 h with a negative correlation but later T led S_{diu} by 3-5 h with a strong positive correlation. With the advent of rains in March, T led S_{diu} with lags of 2-3 h but with strong negative correlations.

499

Figure 6. Boxplots showing seasonal shifts in diurnal lag hours at maximum auto-correlation coefficients (ACF) between SPAC variables: Incoming short-wave radiation (R_s , kW m⁻²), Vapour pressure deficit (VPD, kPa), stand transpiration (T, mm hr⁻¹) and the diurnal component of soil moisture (S_{diu} , mm hr⁻¹). The horizontal dotted line marks zero lag hours. The colour of the boxplot represents the direction of the ACF values.

505

4.4.2. GLS linear regression model for sap flow transpiration

Three contiguous data periods of 9 days and 16 days lengths in winter, and 24 days length in summer were chosen for modeling transpiration in the system (Table 4). The transpiration GLS model with corARMA structure had significantly lower AIC than their respective GLS models without any correlational structure. The model results showed R_s (positive slope) as a significant predictor of T at average values of VPD and soil moisture in winters and the significance of R_s (lower P) increased as the system became progressively drier. Although VPD was not a significant predictor ($P > 0.1$), the coefficient was negative indicating the limiting role played by VPD, especially at higher values. In the summers, VPD (positive slope) became a significant predictor of T under average R_s and S conditions. S was not a significant predictor of T, although it is important to note that soil moisture always remained well above the permanent wilting point of the site. The model performance was affected by the inherent variability in sap flow with complex phenomenon like mid-day depression and pre-dawn sap flux dominating the diurnal movements at the site. However, the model results highlight the shifting roles of R_s and VPD in modulating stand transpiration and thus add to our understanding of plant-water relations in such atypical environments.

521

522 Table 4. Results from Generalized least squares (GLS) linear regression model with corARMA
523 correlational structure for transpiration (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Predictor variables include
524 Incoming short-wave radiation (R_s , kW m⁻²), Vapour Pressure Deficit (VPD, kPa), transpiration (T, mm h⁻¹)
525 and soil moisture (S, mm h⁻¹).

526

527 5. Discussion

528 The study provides the first detailed understanding of plant water-use by cooccurring pioneers and
529 late-successional species in a very wet high elevation tropical broad-leaved evergreen wet montane forest
530 in Eastern Himalaya. We compare the observed plant-water relations with results and mechanisms from
531 other wet tropical montane forests (TMFs). The intra and interspecific variability in sap flow and
532 transpiration are explored across gradients of size, traits, and canopy positioning, and then analyzed in
533 response to environmental drivers and vegetation characteristics of actively growing secondary TMFs.
534 Further, species composition, in terms of functional groups, canopy structure, and phenology exert a strong
535 influence on differential access of vegetation to solar radiation and soil moisture (Ziegler et al. 2009). We
536 discuss their relative roles in explaining the observed intra and interspecific variability in transpiration.

537

538 5.1. Plant-water relations in wet and high elevation Eastern Himalayan TMFs

539 5.1.1. High sap flow rates in wet TMF climatology

540 As mentioned earlier, the study site represents the uniquely wet (MAP = 4500 mm yr⁻¹) and high
541 elevation (2100 masl) Eastern Himalayan habitat. Wet conditions ensure adequate moisture availability
542 throughout the year although seasonal dryness is observed in winters. Similarly, afternoon peaks in
543 precipitation reflect on a limited cloud-free window, which coupled with high elevation, add energy-related
544 constraints on photosynthesis (Kumar et al. 2021). Species under such environments are likely to maximize
545 photosynthesis under moisture abundant conditions, especially the fast-growing pioneers (Lyu et al. 2020).

Not surprisingly, the observed sap flux density (J) in the three species was significantly higher than their respective conspecifics from other TMFs. The observed J in *Castanopsis hystrix* at our site (MAP = 4496 mm) was three times higher than conspecific *Castanopsis tribuloides* from relatively drier (MAP = 1331 mm) Central Himalaya (Ghimire et al. 2014). Similarly, The observed J for *Symplocos racemosa* and *Eurya acuminata* were 6-9 times higher than conspecifics in drier environments: *Symplocos ramosissima* from China (MAP ~2000 mm) and *Symplocos kuroki* and *Eurya japonica* from Japan (MAP ~1700 mm), respectively (Chiu et al. 2016, Zhang et al. 2018). The observations of higher sap flux density and sap flow in pioneers (*S. racemosa* and *E. acuminata*) than late-successional species (*C. hystrix*) has been previously reported from tropical lowland secondary forests (1800 masl) of Panama, Costa Rica (40 masl), mid-elevation Ecuadorian Andes (~2000 masl), and commonly attributed to higher water movement potential of pioneer species (Motzer, Munz, Küppers, and Schmitt 2005, Gutiérrez and Santiago 2006, McCulloh et al. 2011). Consequently, the estimated daily transpiration ($1.45 \pm 1 \text{ mm d}^{-1}$) in relatively wetter Sikkim was also found to be double of drier Central Himalayan oak forests (MAP = 1331 mm) in Nepal (Ghimire et al. 2014), but comparable with wet low elevation (450- 650 masl) TMFs (MAP = 4200-5000 mm) in Costa Rica (Aparecido et al. 2016, Moore et al. 2018) and TMF (MAP = 2067 mm) at comparable elevation in Southern Andes (Motzer et al. 2010). The maximum daily stand transpiration (5.3 mm) is one of the highest among tropical montane or lowland forests (McJannet et al. 2007, Bruijnzeel et al. 2011). Thus, our site exhibited high transpiration despite being at a higher elevation, possibly fueled by faster growth rates and higher interception losses from the secondary forest vegetation in the relatively wetter climate of Eastern Himalaya (Boyce et al. 2012). The observed radial and azimuthal variability in three species confounded the relationship between sap flux density and tree-based scalars like wood properties, tree size, and form, inducing significant scaling errors (Meinzer et al. 2005, Becker et al. 2012, Berry et al. 2018). Sapwood area was found to be a better bio-scalar of tree to stand transpiration than tree diameter and basal area in mixed-species secondary forests (Kumagai et al. 2005, Berry et al. 2018).

570

5.1.2. Nocturnal sap flow and transpiration in Himalayan tree species

571

572 The observed nocturnal transpiration (T_{night}) was similar to studies (~12 %) from China (Siddiq
573 and Cao 2018) and other parts of the globe (Forster 2014, Alvarado-Barrientos et al. 2015) and lower than
574 reports from Mediterranean Europe (35–40 %) (Barbeta et al. 2012). While most of the nocturnal sap flux
575 occurred in the evening, as reported commonly, pre-dawn flux is an uncommon observation from
576 Himalayan TMFs (Forster 2014). The onset timing (0300–0400 h) during days with pre-dawn flux was
577 similar to reports from Mediterranean Europe (Barbeta et al. 2012). The evening sap flux is commonly
578 attributed to stem refilling and thus is a feature of large trees, although not restricted to them (Zeppel et al.
579 2011, Siddiq and Cao 2018). Both evening and pre-dawn sap flux were independent of tree size and other
580 drivers were explored. Our observations of 2–3 h of lag between R_s and VPD and T were seasonally
581 consistent and comparable with reports from TMFs in Costa Rica (Moore et al. 2018) and marginally
582 higher than reports from Tibet (~1-hour lag) (Wang et al. 2017). The lags may represent delays due to low
583 temperature in winters and leaf wetness in the summers due to night rains or dew (Aparecido et al. 2016,
584 Moore et al. 2018). Although summer rains mostly occurred from noon onwards, a significant part also fell
585 in the pre-dawn period (Kumar et al. 2021). Thus, we recommend incorporating leaf wetness as a variable
586 in any future studies in wet TMFs like Eastern Himalaya, which experiences significant summer rains. Pre-
587 dawn sap flux reflected in the opposite trend of T leading R_s and VPD, although the peaks and evening T
588 closely followed R_s and VPD, suggesting that the decoupling between trunk and crown was limited to the
589 pre-dawn period only (Chen et al. 2016).

590 Environmental controls on nocturnal sap flux by VPD, leaf wetness, and soil moisture are well
591 documented (Alvarado-Barrientos et al. 2015, Berry et al. 2016, Siddiq and Cao 2018), whereas
592 endogenous stomatal controls have been reported under hydrated night-time conditions of stable VPD and
593 negligible wind (Resco de Dios et al. 2013, De Dios et al. 2015, Chaves et al. 2016). Concurrent
594 observations of high nocturnal sap flux under low VPD, wind, and moderate soil moisture conditions
595 suggest that circadian-driven stomatal control could be a potential explanation, especially for the pre-dawn
596 flux. Kumar et al. (2021) observe a significant diurnal cycle in summer precipitation which starts from
597 noon leaving a much shorter window of 5–6 h for plant productivity and transpiration. Thus, as proscribed
598 by Barbeta et al. (2012) for Mediterranean Europe, the observed pre-dawn flux could be an adaptation to
599 ensure hydraulic saturation, avoid leaf-level leakage of moisture, and maximise photosynthetic CO_2 at the

600 start of the day. The prevalence across both pioneer and late-successional species suggests that pre-dawn
601 flux could be an adaptation to the wet montane forests and merit further investigations. Being the first
602 observations from Himalayan mountains, pre-dawn sap flux holds significance for future SPAC work in
603 terms of shifting the timing of pre-dawn leaf water potential measurements (Kavanagh et al. 2007),
604 estimating water-use efficiency across species (Chaves et al. 2016), hydrological functioning of these
605 forests (Siddiq and Cao 2018) and regional climate change modeling exercises (De Dios et al. 2015).

606

607 ***5.2. Differential water-use strategies among pioneers and late-successional species***

608 Functional groups played a major role in driving interspecific variability in transpiration. Pioneer
609 species (PS) like *S. racemosa* and *E. acuminata* maintained very high rates of transpiration by maximizing
610 photosynthesis under optimal exposure to solar radiation and soil moisture (Nogueira et al. 2004, Motzer,
611 Munz, Küppers, Schmitt, et al. 2005). Both species also displayed increased radial and azimuthal variability
612 in summers and consistent midday depression. The heightened sensitivity of the pioneer species to
613 environmental extremes is attributed to their canopy position, which exposes them to strong levels of
614 sunlight and VPD triggering midday stomatal closure (Huc et al. 1994, Franco and Lüttge 2002, Chiariello
615 et al. 2006). It is also attributable to their shallow rootedness, although observed topsoil moisture (0-30 cm
616 depth) never went below field capacity. However, pioneer tree species are known to be particularly
617 sensitive to diurnal and seasonal soil moisture fluctuations (Pavlis and Jeník 2000). Seasonal soil moisture
618 stress is known to reduce midday leaf-water potential in Central Himalayan species belonging to the
619 Fagaceae family such as *Castanopsis indica*, *Quercus semicarpifolia*, *Quercus leucotrichophora*, and sub-
620 canopy *Rhododendron arboreum* (Zobel et al. 2001, Poudyal et al. 2004a, Tewari et al. 2018). However,
621 the absence of significant midday depression in deep-rooted species like *C. hystrix* at the peak of the dry
622 season and strong diurnal cycles in soil moisture and streamflow (please refer to Chapter 4 section 3.2.4)
623 provide evidence of vegetation accessing moisture from groundwater (Tanaka et al. 2004, Maeght et al.
624 2013, Allen 2014). The observations add empirical evidence to the discussion on the “two worlds
625 hypothesis” by suggesting that deep-rooted trees can access sub-surface soil moisture if available at
626 shallow levels to fuel transpiration demands (McDonnell 2014, Evaristo et al. 2016). Similar comparison

627 between co-occurring tree species in Semi-arid China has shown high transpiration rates by pioneer
628 species, especially in the growing season (Lyu et al. 2020). The relatively dominant contribution by small
629 and medium-sized trees to T underlines the importance of conducting more sap flow studies on pioneers,
630 especially in diverse tropical secondary forests (Hornbeck et al. 1997, Nogueira et al. 2004, Moore et al.
631 2018).

632

633 ***5.3. Limitations on sap flow in Eastern Himalaya: Energy vs. Moisture***

634 Solar radiation and VPD are two key drivers of transpiration when not constrained by moisture
635 limitations. The study site experienced strong seasonal fluctuations in energy and temperature with
636 moisture and energy-limited winters. This resultant seasonal variability in the relative roles of sunlight and
637 VPD as drivers of T has been reported in other TMFs as well (Moore et al. 2018). We observed that solar
638 radiation was a stronger driver of T than VPD and S in energy-limited winters, similar to report from TMF
639 in Southern Andes (Motzer et al. 2010) and Alps (Fiora and Cescatti 2006), but in contrast to warmer
640 Central Himalaya, where VPD was observed as a stronger driver than solar radiation (Ghimire et al. 2014).
641 However, in summers, VPD became the principal driver of T under abundant energy conditions.

642 Under moisture-abundant and energy-deficient conditions, as in our case, VPD's role as a driver of
643 transpiration can be suppressed by solar radiation. Our observations also provide empirical evidence to the
644 theory that the East Himalayan forests are energy-limited under abundant moisture conditions and solar
645 radiation is a significant driver of non-monsoon vegetation activity, as observed by Sebastian et al. (2019)
646 using remotely-sensed enhanced vegetation index (EVI) as a proxy of vegetation productivity. The role of
647 solar radiation is further accentuated in uneven-aged secondary forests in Sikkim, where the social
648 positioning of the trees in the canopy determines the spatial availability of solar radiation to different parts
649 of the crown (Fiora and Cescatti 2006, Küppers et al. 2008, Zhang et al. 2019). This interactive relationship
650 between secondary forest structure dictating the placement of pioneer and emergent in the forest canopy,
651 diurnal shifts in sunlight availability, and plant water-use in a sloped mountain environment is illustrated in
652 Figure 7.

653

654 Figure 7. Schematic representation of the interactive relationship between placement of pioneer and
655 emergent in the forest canopy, diurnal shifts in sunlight availability and plant water-use in a typical sloped
656 mountain environment in Himalaya.

657

658 **5.4. Influence of secondary forest structure on sap flow variability**

659 The observed Gaussian radial profile with increasing sap flux density in the inner xylem in *C.*
660 *hystrix* is typical of isolated trees with long crown (Fiora and Cescatti 2006). This is ascribed to higher light
661 availability to the older mid-lower portions of the crown anatomically connected to the inner xylem.
662 Conversely, in trees forming a continuous canopy like *S. racemosa* and *E. acuminata* in our case, the lateral
663 foliage activity is suppressed by shading and only the top portion of the crown receives proper light,
664 potentially causing higher sap flux density in the outer xylem. This was highlighted by the overestimation
665 of radial correction factors ($C_h < 1$) by outer xylem of in-canopy pioneers like *S. racemosa* and *E.*
666 *acuminata*, and underestimation by ($C_h > 1$) by outer xylem in emergent trees of *C. hystrix*. Delzon et al.
667 (2004) have observed that the radial correction factors were independent of meteorological factors and
668 better represented the xylem-crown water-use connectivity. Further, in sloped terrains, landscape
669 characteristics like slope and aspect influence diurnal changes in the angle and intensity of incident light,
670 potentially inducing azimuthal variability in sap flow (Kumagai et al. 2007, Chang et al. 2014, Berry et al.
671 2016). Thus, fully exposed crowns of *C. hystrix* exhibited shifting peaks in sap flow from north to south
672 sensors following the NE-SW trajectory of solar radiation, whereas the in-canopy *S. racemosa* and *E.*
673 *acuminata* maintained dominant flow at northern probes. Daytime radial and azimuthal variability across
674 the species were attributed to the interaction between the access to solar radiation and soil moisture,
675 whereas night variability was negatively correlated with VPD (Fiora and Cescatti 2006, Shinohara et al.
676 2013). The biases induced by the failure to incorporate azimuthal and radial variability were found to be
677 significant and similar to other studies (Fiora and Cescatti 2006, Kume et al. 2012, Shinohara et al. 2013).

678

679 **6. Conclusions**

680 It is still challenging to estimate stand transpiration from sap flow measurements in diverse secondary
 681 TMFs because of the variability among different functional groups and diversity in traits that regulate
 682 plant-water relations (Huc et al. 1994, Nogueira et al. 2004, Küppers et al. 2008). Radial and azimuthal
 683 probes opened a whole new dimension to plant-water use for Himalayan species and their use is highly
 684 recommended to reduce errors in estimating stand transpiration (Shinohara et al. 2013, Komatsu et al.
 685 2016). We also highlight the importance of incorporating information on stand structure and tree density
 686 while scaling from individuals to stand-level (Küppers et al. 2008). Regardless, the stand transpiration of
 687 these East Himalayan wet tropical montane broad-leaved forests has been estimated for the first time using
 688 methods covering maximum variability of sap flow using limited resources. Stand transpiration is double of
 689 relatively drier Central Himalaya (Ghimire et al. 2014), but at the lower bound of the values reported from
 690 tropical montane cloud forests globally, indicating the interactive role of precipitation and elevation in
 691 modulating the available energy, moisture, and plant productivity (Bruijnzeel et al. 2011). Owing to the
 692 high elevation and cold conditions, solar radiation emerged as the primary driver of transpiration in winters
 693 and D in wet summers. Significant nocturnal transpiration dominated by the pre-dawn movement is the first
 694 report from the Himalaya. Other adaptations like midday depression in shallow-rooted pioneer species
 695 highlight their sensitivity to soil moisture fluctuations. Yet, the deep-rooted Fagaceae species access deeper
 696 groundwater and transpired unaffectedly.

697 Studies on climate change in Eastern Himalaya have predicted an increase in summer rainfall,
 698 declining winter rains; and increasing summer and winter temperatures (Kulkarni et al. 2013, Sanjay et al.
 699 2017, Krishnan et al. 2019). Our results suggest that drier and warmer winters are likely to impact the
 700 phenology and negatively affect the productivity of shallow-rooted secondary pioneers like *S. racemosa*
 701 and *E. acuminata*, whereas the deep-rooted species like *Castanopsis* spp. and Himalayan oaks may remain
 702 unaffected. The phenological asynchronization can play a critical role in the temporal partitioning of water
 703 within different parts of a tree, and between co-occurring species (Francescantonio et al. 2018). Thus, the
 704 secondary broad-leaved forests, with the dominance of shallow-rooted pioneers, are more prone to the
 705 negative impacts of drier and warmer winters than primary forests, which are dominated by deep-rooted
 706 species. In summers, rains provide enough moisture to ensure peak vegetation productivity in April.

707 However, increased summer precipitation in the future could result in higher cloud cover negatively
708 impacting both vegetation productivity and transpiration leading to increased streamflow in summer (Aston
709 1984, Donohue et al. 2017). Increased summer moisture and cloud cover could also allow the opportunistic
710 fast-growing pioneers to outcompete the late-successional species (Lyu et al. 2020).

711 The overall effect of changes in temperature and precipitation on biodiversity in the region remains
712 complex and requires ecohydrological models specific to the East Himalayan TMFs (Tsering et al. 2010,
713 Asbjornsen et al. 2011). More regional studies inclusive of diurnal and seasonal variability in transpiration
714 will be critical to increasing the accuracy of land-surface interaction models and predicting the impact of
715 climate change on Himalayan ecohydrology (Wang and Dickinson 2012, Miller et al. 2018). It will be
716 worth investigating the role of soil mycorrhizae and root hair densities in facilitating the high transpiration
717 rates observed in these forests (Breda et al. 2006, Carminati et al. 2017). The study provides the first
718 empirical understanding of climatic controls on vegetation water-use from a very wet high elevation
719 tropical broad-leaved evergreen wet montane forest in Eastern Himalaya, one of the 30 global biodiversity
720 hotspots and global 200 ecoregions of importance (Brooks et al. 2006, Chettri et al. 2010). The study
721 contributes to the scant literature on plant-water relations from secondary TMFs where similar species can
722 behave differently than primary forests making generalizations across functional groups, forest types, and
723 climatic conditions highly erroneous (Boyce et al. 2012, Berdanier et al. 2016), and compares the plant-
724 water use strategies between co-existing pioneer and late-successional species (Moore et al. 2018). We
725 recommend prioritizing the conservation and management of these secondary forests in Sikkim for
726 sustained ecosystem services.

727

728 **7. Data and Materials Availability**

729 The data that support the findings of this study are available on request from the corresponding author. The
730 data are not publicly available due to privacy or ethical restrictions. A sample subset of the data that
731 support the findings of this study is available in Dryad at (doi:10.5061/dryad.47d7wm3cg) under the
732 citation Kumar (2021). The sample dataset is available for preview at the following url:

733 <https://datadryad.org/stash/share/bkDWLqnM4S2C3w0wgri1AcXlyDz3eM2Sgs7prOqLZqk>

734

735 **8. Authors' Contributions**

736 Manish Kumar did the execution of the study including study design, including testing and modification of
737 the sap flow probes, field investigation, data processing, formal analysis, and original manuscript writing
738 and editing. Yangchenla Bhutia contributed with the vegetation data for scaling up from tree to stand
739 transpiration and helped in vegetation characterisation and manuscript revisions. Dr. Jagdish
740 Krishnaswamy supervised the overall study and generated the requisite funds and resources. Dr. Gladwin
741 Joseph and Dr. Jagdish Krishnaswamy helped in the conceptualization, sap flow probe designing, field
742 investigation, and reviewing and editing the manuscript.

743

744 **Conflict of interest**

745 The authors have no relevant financial or non-financial interests to disclose.

746

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762

763 **Authors' Contributions**

764 **Manish Kumar:** Conceptualization, Methodology, Manufacturing, Testing and modification of the sap
765 flow probes, Investigation, Software, Formal analysis, Visualization, Writing – Original draft preparations.
766 **Yangchenla Bhutia:** Investigation, Writing – Review & Editing. **Gladwin Joseph:** Conceptualization,
767 Methodology, Testing and modification of the sap flow probes, Writing – Review & Editing. **Jagdish**

768 **Krishnaswamy:** Conceptualization, Methodology, Testing and modification of the sap flow probes,
769 Writing – Review & Editing, Supervision, Project Administration, Funding acquisition.

770

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Figure 7. Pictorial representation of the interactive relationship between placement of pioneer and emergent in the forest canopy, diurnal shifts in sunlight availability and plant water-use in a typical sloped mountain environment in Himalaya.

Tables

Table 1. Life-forms and ecophysiological characteristics of the three species used for sap flow measurements.

Species	Family	Form	Functional group	Canopy position	Rooting depth	Wood type
<i>S. racemosa</i>	Symplocaceae	Small-medium trees	Pioneers	In-canopy	Shallow	Diffuse-porous
<i>E. acuminata</i>	Pentaphylacaceae	Shrubs-small trees	Pioneers	In-canopy	Shallow	Diffuse-porous
<i>C. hystrix</i>	Fagaceae	Large trees	Late-successional	Emergent	Deep	Semi ring-porous

Table 2. Biometric details ($\pm$ standard deviation) of the three species instrumented for sap flow measurements along with the total number of data days and number of radial probes installed per species.

Species	No. of trees	DBH (m)	Basal area	Sapwood area	No. of radial probes/tree	Data (days)
			(m ²)	(m ²)		
<i>S. racemosa</i>	5	0.21 $\pm$ 0.06	0.036 $\pm$ 0.02	0.032 $\pm$ 0.02	5	49
<i>E. acuminata</i>	5	0.19 $\pm$ 0.04	0.028 $\pm$ 0.01	0.026 $\pm$ 0.01	4	87
<i>C. hystrix</i>	3	0.34 $\pm$ 0.2	0.11 $\pm$ 0.12	0.037 $\pm$ 0.02	5	99

Table 3. Estimates of sap flux density (J), whole-tree sap flow (V), tree-to-tree coefficient of variation in sap flow (COV) in the studied species and at stand-level. Percentage biases in whole-tree sap flow (V) estimation due to ignoring radial and azimuthal variability (standard deviation in parentheses) are presented across species and in stand transpiration.

Species	J (cm ³ cm ² hr ⁻¹)	V (kg hr ⁻¹)	Radial bias (%)	Azimuthal bias (%)
<i>S. racemosa</i>	28 (2)	26 (11)	8 (4)	-5 (12)
<i>E. acuminata</i>	21 (10)	15 (8)	1 (3)	5 (12)
<i>C. hystrix</i>	13 (5)	23 (16)	8 (7)	-21 (41)
Stand-level	22 (9)	21 (11)	9 (5)	-16 (24)

Table 4. Results from Generalized least squares (GLS) linear regression model with corARMA correlational structure for transpiration (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Predictor variables include Incoming short-wave radiation (R_s , kW m^{-2}), Vapour Pressure Deficit (VPD, kPa), transpiration (T , mm h^{-1}) and soil moisture (S , mm h^{-1}).

Season	No. of days	Variables	Lag (hours)	Coefficients	Std. Error	t-value	p-value (P)
Winter	9	S	0	-0.008	0.058	-0.145	0.885
		R_s	2	0.187	0.079	2.366	0.019*
		VPD	1	0.182	0.197	0.919	0.359
	16	S	0	0.019	0.032	0.617	0.538
		R_s	0	0.119	0.021	5.574	<0.001***
		VPD	6	-0.003	0.075	-0.039	0.969
Summer	24	S	0	0.004	0.006	0.688	0.492
		R_s	2	0.039	0.035	1.116	0.265
		VPD	2	0.223	0.066	3.401	<0.001***

Supplementary Files

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