

1 **Quantification of hydraulic trait control on plant hydrodynamics and risk of hydraulic**
2 **failure within a demographic structured vegetation model in a tropical forest (FATES-**
3 **HYDRO V1.0)**

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25 **Abstract:** Vegetation plays a key role in the global carbon cycle and thus is an important
26 component within Earth system models (ESMs) that project future climate. Many ESMs are
27 adopting methods to ~~trace the resolve plant~~ size and ~~succession-stage-structure-of-plants~~
28 ~~within ecosystem disturbance history using vegetation~~ demographic models. These models make
29 it feasible to conduct more realistic simulation of processes that control vegetation dynamics.
30 ~~Separately~~ ~~Meanwhile~~, increasing understanding of the ~~ecophysiological~~ processes governing plant
31 water use, and ~~the need to understand~~ ecosystem responses to drought in particular, has led to the
32 adoption of ~~physical~~ ~~dynamic~~ plant water transport (i.e., hydrodynamic) schemes within ESMs.
33 However, the impact of plant hydraulic trait variation in trait-diverse tropical forests is
34 understudied. In this study, we report on a new sensitivity analysis of an existing hydrodynamics
35 (HYDRO) model that is updated and incorporated ~~into~~ the Functionally Assembled Terrestrial
36 Ecosystem simulator (FATES). The size and canopy structured representation within FATES is
37 able to simulate how plant size and hydraulic traits affect vegetation dynamics and carbon/water
38 fluxes. To better understand this new model system and its functionality in tropical forest systems
39 in particular, we conducted a global parameter sensitivity analysis at Barro Colorado Island,
40 Panama. We assembled 942 observations of plant hydraulic traits on 306 tropical plant species for
41 stomata, leaves, stems, and roots, and determined the best-fit statistical distribution for each trait-
42 ~~Our, which was used in model~~ ~~analysis-parameter sampling to assess the parametric sensitivity.~~
43 We showed that ~~the taper component determining~~, for simulated leaf water potential and loss of
44 hydraulic conductivity ~~tapering from trunk to branch~~ across different plant organs, the water
45 potential leading to 50% loss (P_{50}) of four most important traits were associated with xylem conduit
46 taper (buffers increasing hydraulic resistance with tree height), stomatal conductance, the
47 sensitivity to leaf water potential, maximum stem hydraulic conductivity ~~for the stem~~, and the

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48 ~~fraction partitioning~~ of total hydraulic resistance ~~in the above-ground section are the top 5 traits~~
49 ~~determining the simulated water potential and loss above vs. belowground. Our analysis of~~
50 ~~conductivity for different plant organs. For the individual ensemble members revealed that trees at~~
51 ~~a high~~ risk of hydraulic failure and potential tree mortality, ~~we found that ensemble members with~~
52 ~~high risk of mortality~~ generally have ~~a higher taper exponent~~ higher conduit taper, maximum xylem
53 conductivity, stomatal sensitivity to leaf water potential, and a higher xylem conductivity, less
54 ~~negative P_{50} for stomata conductance, and more negative P_{50}~~ lower resistance to xylem embolism
55 for stem and transporting roots. We expect that our results will provide guidance on future
56 modeling studies using plant hydrodynamic models to predict the forest responses to droughts, and
57 future field campaigns that aim to better parameterize ~~the~~ plant hydrodynamic ~~model~~ models.

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59

60 1. Introduction

61 Tropical forests play a critical role in regulating regional and global climates (Bonan,
62 2008). Under ongoing and future climate change, they are subjected to substantial risks of
63 climate extremes such as drought and heat waves (Mcdowell et al., 2018). Studies have already
64 shown that tropical forests were experiencing elevated tree mortality rates due to mega
65 droughts related to ENSO events. For example, the 2015–16 El Niño led to the death of an
66 estimated 2.5 ± 0.3 billion stems in the Lower Tapajós river basin of the Amazon and the
67 associated carbon loss had not yet been compensated by new plant growth three years after the
68 event (Berenguer et al., 2021). ~~Such extreme climate events are projected to increase in~~
69 ~~frequency and intensity under a warming future.~~ Such extreme climate events are projected to
70 increase in frequency and intensity under a warming future (Seneviratne et al., 2021). A
71 statistical analysis based on the projection of 13 ESMS under a high greenhouse emission
72 scenario showed that the frequency of extreme droughts as defined by rhizosphere soil
73 moisture (occurring once every 50 years) could increase by a factor of nearly ~~4~~four and this
74 increase would have ~~substantially more~~ a disproportionate impact on tropical forests (Xu et al.,
75 2019). The high species diversity found in tropical forests may result in increased resilience
76 to climate extremes, based on the demonstrated resilience of temperate forests in relationship
77 to trait diversity (Anderegg et al., 2018). However, due to limited data to
78 ~~parametrize~~ parameterize and constrain models for tropical forests, there is a large uncertainty
79 in our predictive understanding of how tropical forests will respond to these climate extremes
80 (Bonal et al., 2016). This tropical forest uncertainty is ~~considered to be~~ a key source of the

81 global uncertainty in ~~our projection~~projections of land carbon fluxes and future climates (Arora
82 et al., 2020).

83 Earth System Models (ESMs) have been developed to project future changes to the coupled
84 climate and biosphere system. Typically, ‘big leaf’ approximations of vegetation with no
85 explicit presentation of tree size and canopy structure have been used to predict the impact of
86 vegetation on carbon and water cycles. These models do not represent the fundamental
87 elements of vegetation dynamics including growth, mortality, competition, ~~and growth~~, and
88 their response to disturbances. In the last decade, many ESMs have incorporated vegetation
89 demographic models (VDMs) that represent plant size, canopy structure and disturbance
90 histories, with the goal of better representing the competitive dynamics among different size
91 classes of trees and plant functional types in response to climate and ~~vegetation~~
92 ~~disturbance~~disturbances (Fisher et al., 2018). Most of these VDMs can differentiate plants’
93 light, water and carbon use strategies and can thus represent some part of the functional
94 diversity of tropical forests (Massoud et al., 2019; Koven et al., 2020).

95 Following the ‘big leaf’ model, water limitation on plant gas exchange in these VDMs is
96 generally calculated based on three factors: 1) soil water potential; 2) root distribution; and 3)
97 water potential for stomata openness and closure, all of which differ by plant functional
98 ~~types~~types (Koven et al., 2020). While ~~such~~these soil-moisture-dependent water limitation
99 functions are able to capture trait diversity in leaf-level stomatal behaviors, they fail to capture
100 plant functional diversity in many other observable plant hydraulic traits, such as xylem
101 capacitance, water potentials for loss of xylem hydraulic conductivity, stem hydraulic safety
102 margin, and turgor loss point (Hochberg et al., 2018). Many studies have shown that plant
103 hydraulic traits play an important role in plant responses to droughts (Su et al., 2022; Anderegg

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104 et al., 2016), which could shape the landscape distribution of plant functional types (Kunert et
105 al., 2021). In view of this limitation, plant hydrodynamic models have been developed with
106 the aim of better simulating forest response to droughts (Powell et al., 2018; Christoffersen et
107 al., 2016; Xu et al., 2016; Kennedy et al., 2019; Mcdowell et al., 2013). ~~These models not only~~
108 ~~allows us to better incorporate hydraulic functional diversity, but also allow us to~~
109 ~~mechanistically simulate the risk of plant mortality due to hydraulic functional failure resulting~~
110 ~~from embolism in xylem.~~ These models not only incorporate hydraulic functional diversity,
111 but also mechanistically simulate the risk of plant mortality due to hydraulic functional failure,
112 as a result of an inability to move water in the xylem due to embolism in conduits (Hammond
113 et al., 2019).

114 One key challenge for these plant hydrodynamic models is that they have many more
115 parameters than simple water limitation functions based on soil water potentials and thus
116 inherently possess more uncertainty in the model parameterization and subsequent simulations.

117 In this study, we describe the implementation of a hydrodynamic scheme within DOE-
118 sponsored functionally assembled terrestrial ecosystem simulator (FATES-) (Koven et al.
119 2020), and assess this new configuration with two goals: 1) assessquantify the
120 importanceparametric sensitivity of different hydraulic traits in determining plant
121 hydrodynamics; and 2) identify key hydraulic traits that are important for predicting the risk
122 of mortality due to hydraulic failure. We expect that our results will provide guidance on model
123 parameterization for future modeling studies using plant hydrodynamic models to predict
124 tropical forest response to droughts, and future field campaigns that aim to collect
125 observational data that can be used to better parameterize and benchmark plant hydrodynamic
126 models.

127 2. Methodology

128 2.1. Model description

129 We use ~~the functionally assembled terrestrial ecosystem simulator (FATES)~~, FATES, a
130 VDM that is coupled within the Energy Exascale Earth System Model (E3SM) (Caldwell et
131 al., 2019). FATES represents size-structured groups of plants (cohorts) and successional
132 trajectory-based patches using the ecosystem demography approach (Fisher et al., 2015;
133 Moorcroft et al., 2001). FATES simulates growth by integrating photosynthesis across
134 different leaf layers for each cohort. FATES allocates this photosynthate to different tissues
135 including leaves, fine and coarse roots, and stem, based on the allometry of different plant
136 functional types, as well as a carbon storage pool (Fisher et al., 2015). Mortality within FATES
137 is simulated by several mechanisms, including carbon starvation caused by depletion of the
138 storage pool, hydraulic function failure, as well as impact mortality during disturbance, fire,
139 logging, freezing, age-related and ‘background’ constant turnover (Fisher et al., 2015; Huang
140 et al., 2020; Fisher et al., 2010; Needham et al., 2020).

141 2.1.1. Plant Hydrodynamics

142 The default ~~(non-hydrodynamic)~~ FATES model contains a simplistic algorithm that
143 approximates plant hydraulic failure thresholds based on soil water potential. An important
144 feature of the plant hydrodynamic scheme (HYDRO), which explicitly simulates water flow
145 from the soil through leaves to the atmosphere, is that it enables direct representation of percent
146 loss of conductance as a predictor of hydraulic failure mortality rates.- FATES-HYDRO is
147 based on the hydrodynamic model implemented in the Traits-based Forest Simulator (TFS)
148 (Christoffersen et al., 2016).~~The water flow is calculated based on water pressure gradients~~
149 ~~across different plant compartments (rhizosphere, absorbing roots, transporting roots, stem,~~

and leaf), and the features most relevant to the present analysis are summarized below. The model approximates water transport in a single vertical dimension, approximating the canopy as a single leaf layer at the top of a beam, according to the Shinozaki pipe model (Shinozaki et al., 1964) in which the hydraulic path length from the trunk base to each leaf is assumed constant. Following the 'porous media' approach, the model simulates the water transport across four main organs (leaves, stem- trunk/branches, transporting roots, and absorbing roots) and different rhizosphere shells (Fig. 1). Resistors connect the different compartments. Specifically, flow between compartment i and $i + 1$ (Q_i) is given by,

The water flow is calculated based on water pressure gradients across different compartments (rhizosphere, absorbing roots, transporting roots, stem, and leaf). Specifically, flow between compartment i and $i + 1$ (Q_i)

$$Q_i = -K_i \Delta h_i \quad (1)$$

is given by,

$$Q_i = -K_i \Delta h_i \quad (1)$$

where K_i is the total conductance ($\text{kg MPa}^{-1} \text{s}^{-1}$) at the boundary of compartments i and $i + 1$ and Δh_i is the total matric potential difference between the compartments:

$$\Delta h_i = \rho_w g (z_i - z_{i+1}) + (\psi_i - \psi_{i+1}), \quad (2)$$

$$\Delta h_i = \rho_w g (z_i - z_{i+1}) + (\psi_i - \psi_{i+1}), \quad (2)$$

where z_i is compartment elevation difference above (+) or below (-) the soil surface (m), ρ_w is the density of water (10^3 kg m^{-3}), g is acceleration due to gravity (9.8 m s^{-2}), and ψ_i is tissue or soil matric water potential (MPa). K_i is treated here as the product of a maximum boundary conductance between compartments i and $i + 1$ ($K_{max,i}$), and the fractional

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170 maximum hydraulic conductance of the upstream compartments (FMC_i or FMC_{i+1}), which is
171 a function of the tissue water content— as follows,

$$172 \quad FMC_i = \left[1 + \left(\frac{\psi_i}{P_{50,x}} \right)^{a_x} \right]^{-1} \quad (3)$$

173 where ψ_i is the compartmental water potential, $P_{50,x}$ is the water potential at 50% loss of
174 maximum conductivity for different plant tissues (absorbing root, transporting root, stem), a_x
175 is the corresponding vulnerability curve shape parameter, with a larger number indicating a
176 steeper reduction of conductivity in response to more negative water potentials (Choat et al.,
177 2012). The maximum percentage loss of conductivity (PLC) across different organs [i.e., PLC_i
178 $=100 (1-FMC_i)$] is used to measure the risk of tree mortality (M_{hf}) resulting from hydraulic
179 failure as follows,

$$180 \quad M_{hf} = M_{hf,base} \frac{\max(0, PLC_{max,organ} - PLC_c)}{100 - PLC_c} \quad (4)$$

181 where PLC_c is the critical percentage loss of conductivity with risk of mortality, $PLC_{max,organ}$
182 is the maximum percentage loss of conductivity across different organs, $M_{hf,base}$ is the
183 baseline mortality rate [fraction/year] when percentage loss of conductivity exceeds PLC_c . In
184 this version of model, we assume that xylem cavitation can fully recover as long as the trees
185 do not die.

186 The previous version of this model (TFS-Hydro) presented water in terms of relative water
187 content (RWC; $g \text{ H}_2\text{O} \text{ g}^{-1} \text{ H}_2\text{O}$ at saturation) in line with most empirical work on plant water
188 relations. While the underlying equations remain unchanged, here we present water in terms
189 of volumetric water content (θ ; $\text{m}^3 \text{ H}_2\text{O} \text{ m}^{-3}$ plant tissue), since this what is accounted by the
190 model and is consistent with what is tracked in the soil as well. The two quantities are related
191 via the equation $RWC = \theta / \theta_{sat}$, where θ_{sat} indicates saturated volumetric water content. The

192 water potential for tissue x [ψ_x] is related to θ_x (the PV curve) following three stages of water
 193 tissue drainage as follows (Tyree and Yang, 1990; Bartlett et al., 2012).

$$194 \quad \psi_x = \begin{cases} \psi_{0,x} + m_{cap} \left(\frac{\theta_x}{\theta_{sat,x}} - 1 \right) & \theta_{ft} < \theta_x \leq \theta_{sat,x} \\ \psi_{sol}(\theta_x) + \psi_p(\theta_x) & \theta_{tlp,x} < \theta_x \leq \theta_{ft,x} \\ \psi_{sol}(\theta_x) & \theta_{r,x} < \theta_x \leq \theta_{tlp,x} \end{cases} \quad (5)$$

195 Stage one applies to stem and roots only and represents the water draw from capillary reserves
 196 (embolized conduits or airspaces in wood) when wood water content is in between full turgor
 197 ($\theta_{ft} = RWC_{ft} \theta_{sat,x}$) and saturation ($\theta_{sat,x}$) and only represents a small fraction of the total
 198 PV curve. It is linear with constant slope $m_{cap} = 11.3 \text{ MPa m}^3 \text{ m}^{-3}$ and $RWC_{ft} = 0.958$ as
 199 estimated from sapwood PV curves on 28 tropical and subtropical species (Christoffersen et
 200 al. 2016). RWC_{ft} is assumed to be 1.0 in leaves. Xylem water potential is assumed zero at full
 201 saturation. The second stage is between full turgor ($\theta_{ft,x}$) and the turgor loss point ($\theta_{tlp,x}$),
 202 when the xylem water potential is in balance with solute ($\psi_{sol}[\theta_x]$) and pressure water
 203 potential ($\psi_p[\theta_x]$) of living cells. The third stage is after the turgor loss point ($\theta_{tlp,x}$), but
 204 above the point of residual water content ($\theta_{r,x} = RWC_{r,x} \theta_{sat,x}$) where the water potential is
 205 only a function of the solute water potential. $RWC_{r,x}$ is synonymous with the apoplastic
 206 fraction (Bartlett et al. 2012).

207 The solute water potential is given as,

$$208 \quad \psi_{sol}[\theta_x] = \frac{\pi_0(\theta_{sat,x}RWC_{ft} - \theta_{r,x})}{(\theta_x - \theta_{r,x})} \quad (6)$$

209 where π_0 is the tissue osmotic potential at full turgor. The pressure potential is calculated as
 210 follows,

$$211 \quad \psi_p[\theta_x] = -|\pi_0| + \varepsilon \frac{(\theta_x - \theta_{sat,x}RWC_{ft})}{(\theta_{sat,x}RWC_{ft} - \theta_{r,x})} \quad (7)$$

212 where ε is the bulk elastic modulus (MPa).

213 The realized conductivity of the above ground portion of the plant per unit of leaf area ($K_{l,max,tree,ag}$) is calculated based on xylem hydraulic conductivity at petiole ($k_{s,max,petiole}$),
 214 aboveground tree height (H, meters), and a xylem taper factor (X_{tap}) as follows.

$$215 \quad \underline{K_{l,max,tree,ag} = \frac{k_{s,max,petiole}}{H(\frac{A_l}{A_s})} X_{tap}} \quad (8)$$

216 where $k_{s,max,x}$ is the maximum xylem conductivity per unit sapwood area, $\frac{A_l}{A_s}$ [i.e., la2sa in
 217 Table 1] is the ratio of leaf area (A_l) to sapwood area (A_s). X_{tap} is the xylem taper factor
 218 representing the ratio of aboveground xylem conductance with taper to that without, which for
 219 intermediate values of conduit taper ($p_{taper} = 1/6$; see below) represents a factor increase in
 220 total conductance of 23–50 for trees of heights 10–30 meters (Christoffersen et al., 2016).
 221 Savage et al. (2010) highlighted how opposing selective forces will both increase hydraulic
 222 conductance by the tapering of conduit radii ($p_{taper} > 0$) while at the same time protect
 223 against embolism by minimizing conduit taper (no taper implies $p_{taper} = 0$). They defined
 224 p_{taper} as the exponent on an external branching parameter (2 daughter branches per parent
 225 branch in their model) that sets the degree of internal branching of xylem conduits (and thus
 226 the tapering of conduit radii as well) and, using a fractal network model, derived an effective
 227 exponent q that describes how aboveground conductance increases with tree size. q is a
 228 monotonically increasing and saturating function of the taper exponent p (see Fig 2b of Savage
 229 et al. 2010); we used this relationship to estimate q , and thus X_{tap} in eq. (8) as

$$230 \quad \underline{X_{tap} = \left[\frac{r_{base}}{r_{petiole}} \right]^{q_{tap} - q_{notap}}} \quad (8)$$

231 where r_{base} and $r_{petiole}$ are the trunk and petiole radii, respectively. The ratio $r_{base}/r_{petiole}$ is
 232 related to tree height following the fractal tree model of Savage et al. (2010) (see equations
 233 S12-S13 in Christoffersen et al. 2016).
 234

Eq. (8) only gives the aboveground component of whole-plant conductance. In the absence of a simple first-principles approach to estimating the belowground component, we estimate the total tree maximum conductance (above- and belowground components) as

$$K_{max,tree,total} = R_{frac,stem} K_{max,tree,ag} \quad (9)$$

where $R_{frac,stem}$ is the fraction of total resistance that is aboveground.

Stomatal conductance [g_s , $\mu\text{mol m}^{-2} \text{s}^{-1}$] is simulated through a modified Ball-Berry equation.

$$g_s = g_0 + g_1 \frac{A_n}{C_s/P_{atm}} h_s \quad (10)$$

where g_1 is the stomatal conductance slope in response to environmental condition changes, g_0 is the minimum (cuticular) stomatal conductance ($\mu\text{mol m}^{-2} \text{s}^{-1}$), C_s is the leaf surface CO_2 partial pressure (Pa), P_{atm} is the atmospheric pressure (Pa), h_s is the leaf surface humidity, and A_n is leaf net photosynthesis rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Stomatal conductance is further modified by a plant water stress factor, β , calculated as

$$\beta = \left[1 - \left(\frac{\psi_{leaf}}{P_{50,gs}} \right)^{a_{gs}} \right]^{-1} \quad (11)$$

where ψ_{leaf} is the leaf water potential, $P_{50,gs}$ is leaf water potential at 50% loss of maximum stomatal conductance, and a_{gs} is the stomatal vulnerability shape parameter.

The total fine root surface area affects the amount of water a plant can take up through its influence on rhizosphere conductance and is determined by both the specific root length (srl) and absorbing root radius (rs_2). Specifically, the model has a specified number of soil shells (5 in this study) around fine root surfaces and the conductance between soil shell $k+1$ and k , $K_{shell,k}$, is calculated as,

$$K_{shell,k} = K_s \frac{\pi l_{aroot,common}}{\ln(r_{k+1}/r_k)} \quad (12)$$

where r_k is the mean radi of k th shell, $l_{aroot,common}$ is the total length of absorbing roots calculated as a product of total fine root biomass and specific root length (sr_l). K_s is set to be the conductance for soil (K_{soil}) when $k > 1$. For $k = 1$,

$$K_s = \frac{1}{\frac{1}{K_{soil}} + \frac{1}{K_{root,soil}}} \quad (13)$$

where $K_{root,soil}$ is the conductance between fine root surface and soil. An update to the TFS-Hydro approach is to make this conductance direction-specific, in view that water loss rate from root could be substantially lower than water uptake rate either through osmotic regulation (Dichio et al., 2006) or by lacunae caused by rupture of cortical cells (North and Nobel, 1992) during drought. It is determined by either the maximum uptake of water per unit of absorbing root surface area ($k_{r1,max}$, $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) when root water potential is more negative than adjacent rhizosphere soil water potential, or the maximum root water loss rate per unit surface area ($k_{r2,max}$, $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) when rhizosphere water potential becomes more negative than root water potential, which may occur, for example, in frozen soils or in very dry soil layers (Schmidhalter, 1997).

The plant hydrodynamic representation and numerical solver scheme within FATES-HYDRO follows the 1-D solver laid out by Christoffersen et al. (2016), which is the default solver in FATES-HYDRO and used in this study. The model also has an option of a 2-D solver, which is slower and detailed by Fang et al. (2022) and Lambert et al. (2022). 2016). The equations are solved for tissue water content at a 30 minutes time step. We made a few modifications to accommodate the multiple-soil layers and improve the numerical stability. First, to accommodate the multiple-soil layers, we sequentially solve the Richards' equation for each individual soil layer, with each layer-specific solution proportional to each layer's contribution to the total root-soil conductance. Second, to improve the numerical stability, we

280 now linearly interpolate the pressure/volume curve beyond the residual and saturated tissue
281 water content to avoid the rare cases of overshooting in the numerical scheme under very dry
282 or wet conditions. ~~Please~~see the Supplementary Information
283 [HYDRO_DESCRIPTION.pdf] for further details of the implementation.

284 **2.1.2. Non-hydrodynamics processes**

285 FATES-HYDRO can be coupled to different host land models (HLMs) including the
286 E3SM land model (ELM) (Caldwell et al., 2019) or the Community Terrestrial Systems Model
287 (CTSM) (Lawrence et al., 2019). In this study, the model is coupled to ELM. In this section,
288 we layout the key non-hydrodynamic processes in the FATES or the ELM for a better
289 understanding of parameter importance in the results.

290 Canopy radiative transfer is calculated using a multi-layer scheme based on the iterative
291 Norman radiation scheme (Norman, 1979). Leaf and stem area is binned into a matrix of
292 canopy layer, leaf layer and plant functional types. Reflectance, absorption, and transmittance
293 are calculated for each leaf layer. Between canopy layers, light streams are averaged between
294 plant functional types (PFTs), such that all PFTs in understory layers receive equal radiation
295 on their top leaf layer. Fractional absorption of visible and near infra-red light is calculated
296 separately for direct and diffuse light. For the direct stream, transmitted and reflected light is
297 converted into diffuse fluxes. In FATES, the absorbed PAR is used to calculate photosynthesis
298 rates for each of the canopy layer x leaf layer x PFT bins, after which rates across layers are
299 re-aggregated into cohort level carbon fluxes. Please see the Supplementary file in Fisher et al.
300 (2015) for details.

301 The energy balance is handled by the host land model. In this study, it is based on the land
302 component of DOE's Exascale Energy Earth System Model (E3SM). The E3SM land model

303 (ELM) is based on the Community Land Model 4.5 (Oleson, 2013). Specifically, in ELM, the
304 average canopy temperature is calculated based on the energy balance of latent heat, sensible
305 heat, and absorbed radiation as determined by the radiative transfer model. The latent heat is
306 determined by the transpiration, which is determined by the vapor pressure deficit from inside
307 of leaf to the air, canopy stomatal conductance, and boundary layer conductance. FATES
308 calculated mean canopy stomatal conductance averaged across different cohorts, which is fed
309 to ELM to calculate the energy balance. The Newton-Raphson numerical scheme is used to
310 solve for the canopy temperature.

311 All aspects of soil water balance (infiltration, water transfer among soil layers, and
312 drainage) happen at the ‘column’ scale at 30-min time steps and are handled within the Host
313 Land Model (see Oleson et al. 2013 for a detailed description of hydrology in CLM4.5, the
314 parent model of ELM). FATES-HYDRO handles soil water operations at the patch and cohort
315 scales. It simulates root water uptake and changes in plant water potential from roots to leaves
316 based on current time step transpiration. The belowground conductance for each soil layer is
317 weighted by root biomass with an exponential vertical distribution. Sections 2 and 3 in the
318 Supplement of this manuscript provide full details on boundary conditions, sequence of
319 operations among HYDRO and the HLM, downscaling of soil moisture to rhizosphere shells,
320 and downscaling of transpiration from the patch to individual scale.

321 2.2. Sensitivity analysis

322 ~~In this study, as our focus is on the plant hydrodynamics, we used the static stand structure~~
323 ~~mode of FATES that turns off the processes of competition, growth and mortality, to instead~~
324 ~~hold the ecosystem structure constant. This reduced complexity configuration (Fisher and~~
325 ~~Keven, 2020) thus exercises only the primarily fast timescale processes of photosynthesis,~~

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326 ~~transpiration, water transport, and plant hydrodynamics (i.e., change in hydraulic conductivity,~~
327 ~~water storage, and water potentials in plant tissues). By using static stand structure mode, as in~~
328 ~~Chitra Tarak et al. (2021), we isolate hydraulic trait controls on simulated hydrodynamics and~~
329 ~~avoid confounding, and potentially biased, feedbacks from resulting changes in forest~~
330 ~~structure. The forest stand structure include tree size and composition is initialized based on~~
331 ~~the forest inventory data in 2017. As the majority of species in BCI is evergreen broad leaf~~
332 ~~trees, we run the model with one PFT with different hydraulic traits (Table 1) to assess their~~
333 ~~impact on the hydrodynamically relevant outputs including water potentials and fraction of~~
334 ~~maximum conductivity for different plant organs including absorbing root, transporting root,~~
335 ~~stem, and leaves and risk of hydraulic failure. FATES simulates the carbon and water fluxes~~
336 ~~for different size classes of trees. Because large trees experience more fluctuation in~~
337 ~~environmental conditions in the canopy, here we focused on hydrodynamic behaviors for trees~~
338 ~~of diameter more than 60 cm.~~

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339 **2.2. Parametric uncertainty estimation**

340 We identified ~~3635~~ parameters for the FATES-HYDRO model ~~to conduct the parametric~~
341 ~~sensitivity analysis~~ (Table 1). To estimate the parameter distributions, we started with
342 published meta-analyses (Christoffersen et al., 2016; Choat et al., 2012; Bartlett et al., 2012;
343 Bartlett et al., 2014; Bartlett et al., 2016; Klein, 2014) and supplemented them with select new
344 data from individual studies. Focal data were tissue- or individual-level hydraulic traits
345 spanning water transport and embolism resistance, tissue water storage and retention (PV curve
346 traits), hydraulic architecture (i.e., leaf area to sapwood area ratio), stomatal responses to
347 dehydration, and fine root traits (Table 1). For each dataset, we standardized taxonomic names
348 using the TNRS package in R (Boyle et al., 2013). This allowed us to join datasets together

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349 based on species, averaging multiple observations per species if necessary, resulting in a
350 species-specific sparse matrix of all hydraulic traits for all databases and individual studies that
351 we compiled. This pantropical hydraulic trait dataset is included in the Supporting Information
352 [traits_master_trop.csv].

353 ~~We then determined parametric~~

354 This trait dataset consisted of anywhere from 1 - 323 observations for each trait, where
355 each observation corresponds to a different species (multiple observations for the same species
356 are first averaged; see above). Before fitting distributions which best fit the trait to these data-
357 ~~Where necessary, some~~ traits were first transformed to be positive, ~~and certain traits with well-~~
358 ~~defined (e.g., P50) or normalized within [0, 1] when~~ upper and lower bounds were ~~normalized~~
359 ~~on [0, 1] according to $(x - x.lowerbound)/(x.upperbound - x.lowerbound)$ for trait x well-~~
360 ~~defined~~ (Table 1). ~~For~~ Then, for each trait separately, we used ~~parameter estimates for the the~~
361 fitdistr package in R to estimate best-fit parameters for uniform, beta, normal, lognormal, and
362 gamma statistical distributions in order to estimate central tendencies and spread for each trait.
363 The distribution with the largest log likelihood among all possible distributions using fitdistr
364 package in R, and best-fit parameters are given in Table 1. Each model simulation consisted
365 of a single PFT: all trees (across all cohort sizes and patches) had the same traits.

366 We augmented observations with extratropical data to increase sample size for traits with
367 less than three tropics-specific observations. ~~Where~~ When trait data observations were ~~mostly~~
368 ~~unmeasured~~ not present, we used a uniform distribution bounded on our best estimate of the
369 theoretical range (Table 1). As there is limited data on roots, we used the same distribution as
370 that for branches if data ~~was missing~~ were lacking. Because our goal is to understand the model
371 behaviors as determined by different hydraulic traits, we assumed independence among traits.

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372 As we focused on the hydraulic traits in this study, we used non-hydraulic trait values based
373 on an optimal set of parameters that best fit observed water and carbon fluxes in a set of FATES
374 implemented simulations run without hydrodynamics (Koven et al., 2020).

375 2.3.1.1. Sensitivity analysis

376 We used the Fourier Amplitude Sensitivity Test (FAST) to assess the relative importance
377 of parameters in determining the variance of model outputs (Xu and Gertner, 2011a). The main
378 idea of FAST is to assign periodic signals in the sampled parameter values and use Fourier
379 transformation to identify the signals in the outputs. Sampled parameter values are based on
380 Latin hypercube sampling from the fitted statistical distributions (see previous section for more
381 details). We ran 1000 ensemble simulations of the FATES-Hydro to derive model outputs of
382 water potential and fraction of maximum conductivity. For each ensemble simulation, each
383 plant hydraulic trait was assigned with a random draw from each trait's distribution, and the
384 samples for different traits are randomly combined to sample the observed plant hydraulic trait
385 space for sensitivity analysis.

386 We used the Uncertainty Analysis and ~~Sensitivity~~Sensitivity Analysis (UASA) tool
387 (<https://sites.google.com/site/xuchongang/uasatoolbox>) to estimate the parameter
388 importanceparametric sensitivity index, which is ~~defined as~~calculated based on the
389 proportion ratio of ~~total~~the partial variance in the model output ~~variance contributed by~~
390 individualattributed to a specific parameter to the total variables in the model
391 parametersoutput. For details, please refer to Xu and Gertner (2011a). We ~~run~~ran the model
392 with 1000 ensemble members, in view that an order of 100 times effective important number
393 of parameters, which we estimate to be ~10, is needed to achieve reasonable precision (Xu and
394 Gertner, 2011b).

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2.4.2.3. Study area ~~and climate drivers~~

In this study, we used Barro Colorado Island (BCI), Panama, as our test site to evaluate model behavior. We chose BCI ~~as because~~ it has moderately strong dry and wet seasons that allow us to assess the hydrodynamics under different levels of water availability. Moreover, extensive field campaigns in recent years have provided comprehensive data needed for model parameterization, initialization and climate drivers. Finally, we also leverage prior FATES studies of non-hydraulic parameters at BCI (Koven et al., 2020).

BCI has an annual mean temperature of 26.3°C and an annual mean precipitation of 2656 mm with a strong seasonal precipitation signal. The dry season lasts from January to April, with a mean precipitation of 228mm, while the wet season lasts from May-December with a mean precipitation of 2428mm (Paton, 2020). In this study, we used hourly in-situ climate data from 2008-2016 to drive the model. To run the model to equilibrium (in terms of soil moisture content) takes 5-6 years, thus we choose February of 2016 as the target for analysis of dry season hydrodynamics and August of 2016 as the target for analysis of wet season hydrodynamics. ~~Using static stand structure mode means that we do not need to spin up vegetation state and thus reducing the simulation time.~~

2.4. Model setup

In this study, as our focus is on the plant hydrodynamics, we used the static stand structure mode of FATES that turns off the processes of competition, growth and mortality, to instead hold the ecosystem structure constant. This reduced-complexity configuration (Fisher and Koven, 2020) thus exercises only the primarily fast-timescale-processes of photosynthesis, transpiration, water transport, and plant hydrodynamics (i.e., change in hydraulic conductivity, water storage, and water potentials in plant tissues). By using static stand structure mode, as in

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418 Chitra-Tarak et al. (2021), we isolate hydraulic trait controls on simulated hydrodynamics and
419 avoid confounding, and potentially biased, feedbacks from resulting changes in forest
420 structure. Using static stand structure mode also means that we do not need to spin up
421 vegetation state, thus reducing the simulation time. The forest stand structure, consisting of
422 tree size and composition for each patch, is initialized based on forest inventory data collected
423 in 2015 (<http://ctfs.si.edu/webatlas/datasets/bci/>). As the majority of species in BCI are
424 evergreen broad leaf trees, we ran the model with one PFT with different hydraulic traits (Table
425 1) to assess their impact on the hydrodynamically relevant outputs including water potentials
426 and fraction of maximum conductivity for different plant organs including absorbing root,
427 transporting root, stem, and leaves.

428 One key benefit of utilizing a hydrodynamic model is its ability to simulate the risk of
429 hydraulic failure by considering the loss of conductivity in various plant organs. As FATES
430 model was ran on static stand mode, we did not specifically simulate the tree mortality resulting
431 from the hydraulic failure as shown in Eq. (4). Instead, we used the maximum of loss of
432 conductance across the continuum of plant nodes [i.e., $PLC_{max,organ}$ in eq. (4)] to assess the
433 hydraulic failure risk. If $PLC_{max,organ}$ reaches critical threshold PLC_c , which is set to 50%
434 (Adams et al., 2017), trees are assumed to be faced with a high risk of mortality. Using the
435 ensemble simulations, we also aim to identify the most vulnerable plant organs and the critical
436 parameters that influence the likelihood of hydraulic failure.

437 FATES simulates the carbon and water fluxes for different size classes of trees. The forest
438 has 137 cohorts with diameters ranging from 10 cm to >2 meters and height ranging from 1 to
439 38 meters (see Fig. S1 for size distributions). Because large trees experience more fluctuations
440 in environmental conditions in the canopy and higher risk of mortality due to drought (Bennett

441 [et al., 2015](#)), we focused on hydrodynamic behaviors for large trees with diameter at breast
442 height (DBH) more than 60 cm; however, for comparison, we also derived the sensitivity for
443 [smaller trees with DBH less than 60 cm](#).

444 3. Results

445 Our results showed that the simulated ranges across the ensemble of leaf water potential
446 (Fig. 42) and loss of conductivity (Fig. 23) are large. For leaf water potential [of large trees with](#)
447 [diameter > 60 cm](#), the 95% percentile ranges are from -5 MPa to -0.5 MPa and -3 MPa to -0.5
448 ~~MPa~~MPa for February ([dry](#)) and August ([wet](#)) 2016, respectively. Correspondingly, the
449 fraction of maximum stem hydraulic conductivity is much higher during August compared to
450 February (Fig. 23); however, in both months, the modeled range spans almost the full range of
451 between 0 and 1. [For smaller trees with diameter less than 60 cm, our results show that smaller](#)
452 [tree experienced less negative water potential \(Fig. S2 and Fig. 2\) and lower loss of hydraulic](#)
453 [conductivity \(Fig. S3 and Fig. 3\)](#).

454 Based on the FAST sensitivity indices (i.e., the variance in model output contributed by
455 different parameters), the key parameters that control the water potentials of different plant
456 organs (leaf, stem and root) [for large trees \(diameter >60 cm\)](#) include the taper exponent for
457 hydraulic conductivity (p_{taper}), the water potential leading to 50% loss of stomatal
458 conductance ($p50_{gs}$), maximum hydraulic conductivity for the stem ($kmax_{node_stem}$), and
459 the fraction of total hydraulic resistance in the above ground section ($rfrac_{stem}$), in decreasing
460 order (Fig. 34). For the fractional loss of conductivity, the most important parameter is the
461 water potential leading to 50% loss of hydraulic conductance (P_{50}) for the corresponding
462 organs (Fig. 45). Other important parameters are similar to those for simulated water potentials.
463 Notably, the organ-specific P_{50} values are more important for the dry month (February)

464 compared to the wet month (August). For the wet month of August, p_taper is the dominant
465 parameter controlling the pre-dawn and midday loss of hydraulic conductivity, while organ-
466 specific P_{50} parameters are the second most important. For smaller trees with diameter less
467 than 60 cm, the corresponding parametric sensitivity patterns are similar to those of larger trees
468 (Fig. S4 and Fig. S5); however, compared to larger trees, the parametric sensitivity of p_taper
469 for simulated leaf water potential becomes lower for smaller trees (Fig. 4 and Fig. S4).

470 In terms of the risk of hydraulic failure, out of the 1000 ensemble members, ~40-60% of
471 the simulations for February and ~60% of simulation for August suggest that branches are the
472 most vulnerable plant organ, based on highest loss of conductivity across the continuum from
473 root to branch (Fig. 56). For the dry month of February, roots are at greater risk in comparison
474 to the wet season. If we consider the loss of conductivity more than 50% for February 2016 as
475 a threshold for a high risk of mortality (Adams et al., 2017), then 53% of ensemble simulations
476 reach this threshold. The key parameters affecting the risk of mortality, as measured by
477 percentage difference in parameter values for ensemble members reaching 50% loss of
478 conductivity or not, include the water potential leading to 50% loss of conductance for stomata
479 ($p50_gs$), stem ($p50_node_stem$), and transporting roots ($p50_node_root$), maximum
480 hydraulic conductivity of stem ($kmax_node_stem$), and the taper exponent (p_taper) (Fig. 67).
481 Ensemble members with high risk of mortality generally have a higher p_taper and
482 $kmax_node_stem$, less negative $p50_gs$, and moreless negative $p50$ for stem and transporting
483 roots (Fig. 78).

484 4. Discussion

485 Our analysis showed the importance of key plant hydraulic traits in simulating plant water
486 potential and risk of hydraulic failure. This analysis identifies these parameters as potential

487 targets of either model calibration or targeted measurement campaigns to achieve realistic
488 simulations. In our sensitivity analysis, the most influential parameter for both water potential
489 and loss of conductivity is the tapering of the radius of conduit with increasing plant height
490 (p_taper). ~~As p_taper increases, the conduit radius increases from the top of the tree to its~~
491 ~~base. According to Hagen-Poiseuille's equation, this increases the theoretical maximum total~~
492 ~~conductance. Low values of p_taper thus limit the adverse effects of tree height by increasing~~
493 ~~k_max along the whole continuum and reducing the soil-to-leaf water potential needed to~~
494 ~~maintain transpiration. Our inference is that p_taper represents an overarching property of~~
495 ~~plant architecture that influences the relative effect of each of the other ~~parameters with regard~~~~
496 ~~to hydraulic safety and efficiency. While p_taper is less directly related to plant adaptations to~~
497 ~~drought, the architecture of the plant itself determines the range of values that give rise to~~
498 ~~drought adaptive strategies. traits related to hydraulic safety and efficiency (Olson et al., 2021).~~
499 The xylem architecture as determined by p_taper parameter could change in response to age
500 and development stages (Rodriguez-Zaccaro et al., 2019), which is not considered in this study.
501 Future studies evaluating the importance of this change to hydraulic functions could be useful
502 to guide size-dependent growth and mortality. Another dimension of the hydraulic architecture
503 with a critical role in determining both water potential and loss of conductivity, though to a
504 much lesser degree, was the fraction of total tree resistance ~~within that is belowground (i.e., of~~
505 ~~the above-ground stem (entire transporting and absorbing root system; $1 - rfrac_stem$).~~
506 Generally, a plant will ~~maintain this resistance, matching~~ match the growth of its trunk and
507 crown ~~height~~ to maintain ~~total a degree of equilibrium in aboveground~~ resistance as the distance
508 water needs to travel increases (Yang and Tyree, 1993). In this study, due to the lack of data
509 on the belowground resistance, we assigned a quite large range for this trait, which could be

510 ~~impacted~~ impacted by many factors such as belowground root biomass, root network architecture,
511 and ~~interaction~~ interactions between ~~root~~ roots, fungi and bacteria- (Poudel et al., 2021; Bhagat
512 et al., 2021).

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513 The second most sensitive parameter in determining loss of conductance was the leaf water
514 potential at 50% loss of stomatal conductance (*p50_gs*). ~~The~~ This parameter controls the water
515 loss rate from ~~leaf and~~ leaves, with a less negative value ~~provides~~ providing protection from
516 hydraulic failure during water-limited periods. ~~The~~ *p50_gs* trait has been shown to play a
517 key role in tree survival during severe droughts (Breshears et al., 2009; Rowland et al., 2015).
518 The ability to withstand lower leaf water potentials is also a key indicator of sapling and
519 seedling survival during drought and determines species distribution across a moisture gradient
520 (Kursar et al., 2009). There may be a trade-off between drought tolerance (with a lower *p50_gs*)
521 and drought avoidance (a less negative *p50_gs* but with a high capacitance; the amount of
522 water released from reserves as leaf water potential declines), a crucial aspect in determining
523 species drought resistance (Pineda-Garcia et al., 2013). Additionally, loss of conductivity was
524 sensitive to the water potential at 50% loss of max conductivity within the stem (*p50_stem*) as
525 it can largely affect the whole plant conductance and thus the water supply to the leaves.
526 *p50_stem* negatively correlates with wood density and may be a marker of the trade-off
527 between hydraulic efficiency and safety within the stem (Chen et al., 2009; Manzoni et al.,
528 2013). ~~Even though we did not consider; however, other studies have shown that~~ this trade-
529 off ~~as we mainly focused on is weak (Gleason et al., 2016). Liang et al (2019) showed that~~ the
530 ~~hydraulic traits in this study, strength of~~ this trade-off could be ~~important to consider for~~
531 ~~competitions and co-existence among different plant functional types dependent on specie's~~
532 drought strategies.

533 Leaf water potential and loss of conductance were both sensitive to the maximum xylem
534 conductivity in the stem ($kmax_node_stem$). Higher maximum conductivity represents greater
535 xylem efficiency, which in the absence of drought or light limitations would result in greater
536 potential photosynthesis and less negative water potentials (Gleason et al., 2016). However,
537 xylem with higher $kmax_node_stem$ could be more vulnerable to embolism as water potential
538 declines (Sperry and Love, 2015). In tropical rainforests, species with higher conductivity per
539 unit leaf area generally are less desiccation-tolerant, and thus exhibit higher mortality rates
540 (Kursar et al., 2009). Low $kmax_node_stem$ along with high leaf-to-sapwood area ratio ($la2sa$)
541 also represents a vulnerability to reduced conductance which increases with height
542 (Christoffersen et al., 2016).

543 Traits with lower order of impacts on water potential modulate the amount of stored water
544 available during drought. ~~The fraction of water in the capillary reserve within the stem (f_{cap})~~
545 ~~determines the amount of water stored within the stem. Water storage in the stem has been~~
546 ~~shown to help maintain higher water potentials as drought continues (Bartlett et al., 2019).~~ The
547 bulk modulus of elasticity in the root ($epsil_node_aroot$) ~~together with root saturated water~~
548 content determines the amount of water available from cellular storage between complete
549 hydration and loss of turgor (Powell et al., 2017). This represents the ability of the roots to
550 continually supply water to the rest of the plant as drought occurs. It also represents an
551 investment in cellular structure, which may be an additional indicator of adaptations with non-
552 hydraulic origin. The residual water content in the stem ($resid_node_stem$) determines the
553 minimum amount of water xylem will hold and thus impact the amount of water storage plant
554 can use during drought as well (Bartlett et al. 2012). In this study, we made the assumption
555 that the traits are independent of each other, in order to understand the hydrodynamic behaviors

556 of FATES-HYDRO for different hydraulic traits based on a single PFT. Understanding the
557 trade-offs between these traits is crucial for determining the competition among different PFTs.
558 Future studies would greatly benefit from assessing the significance of these trade-offs to
559 predict vegetation dynamics under future climate change.

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560 -In contrast to the majority of hydraulic traits in the model, conduit taper, the fraction of
561 total resistance belowground, and the leaf to sapwood area ratio are whole-plant hydraulic
562 traits. Our analysis highlights the importance of whole-plant hydraulic traits such as conduit
563 taper relative to tissue-level hydraulic traits for a range of plant hydraulic functions, including
564 whole-plant conductance and hydraulic failure risks. An important area for future work is to
565 better constrain and understand the consequences of intra- and interspecific variation in these
566 whole-plant hydraulic traits in tropical forests. Our choice of the range of variation in the
567 conduit taper exponent came from a study on temperate species, and was broad, encompassing
568 the entire range of observed values in that study (Savage et al. 2010). Further, we estimated
569 the effects of variation in the taper exponent on whole-plant conductance conditional on trees
570 following a simple set of optimality assumptions (space-filling, area-conserving, and self-
571 similar branching network structure). However, in practice, such assumptions are often not met
572 (Smith et al., 2014). Therefore, it is possible that the model sensitivity to xylem taper in terms
573 of whole-plant hydraulic function are overestimated. Nevertheless, our study highlights the
574 importance of better constraining this parameter as well as further experimentation with
575 alternate model structures to better account for non-optimal trees in tropical forests.

576 The sensitivity of vegetation to drought stress and hydraulic-failure-induced mortality is
577 of paramount importance for understanding how ecosystems may respond to shifting
578 temperature and rainfall patterns under a changing climate (Mcdowell et al., 2022). We

579 recognize that parametric sensitivity could be different for different sites depending on climate
580 driver, soil moisture and vegetation types. However, we expect the main parameter of
581 importance ~~could be~~ could be useful to guide model calibration to select the candidate
582 parameters for different sites. As understanding of plant hydrodynamics increases, linking
583 model predictions to observable plant traits has emerged as a promising means of constraining
584 predictions of ecosystem resilience. Such traits are challenging and costly to measure in the
585 field and thus resources must be directed carefully when planning measurement campaigns.
586 The identified parameters in this study could provide guidance on the limited measurement we
587 could target in the field.

588 **5. Acknowledgment**

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591 Environmental Research. [RF acknowledges funding by the European Union's Horizon 2020](#)
592 [\(H2020\) research and innovation program under Grant Agreement No. 101003536 \(ESM2025](#)
593 [– Earth System Models for the Future\) and 821003 \(4C, Climate-Carbon Interactions in the](#)
594 [Coming Century\).](#)

595 **6. CODE and Data Availability**

596 The FATES-HYDRO code is available from <https://doi.org/10.5281/zenodo.7686333>. The
597 traits data are in the supplementary file [traits_master_trop.csv].

598 **7. Supplement Information**

599 ~~Two~~Three supplementary file are included. The HYDRO_DESCRIPTION.pdf provide the
600 summary of the hydrodynamic implementation that is different from Christoffersen et al.

601 (2016). The traits_master_trop.csv file include all the hydraulic traits we assembled for the
602 tropical region. [The supplementary figure.pdf provides additional figures for the main text.](#)

603 **8. Author contribution**

604 CX and BC designed the sensitivity analysis experiments. BC collected the data and fitted
605 the trait distributions. CX conducted the analysis and drafted the manuscript. BC, CX, RF, RN
606 and CK designed the implementation of ~~HDRO~~HYDRO codes. -BC implemented the majority
607 of ~~HDRO~~HYDRO codes with code improvement made by CX and RN.- ZR conducted the
608 ensemble model simulations. MS provided the leaf cuticular conductance data. NM, CK and
609 LK provided guidance on the sensitivity analysis, code development and trait data synthesis.
610 All authors contributed to manuscript writing by providing edits and suggestions.

611 **9. Competing interests**

612 The contact author has declared that none of the authors has any competing interests.

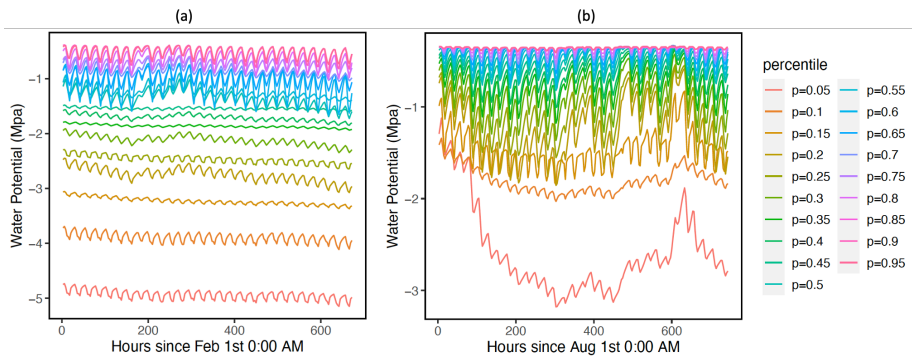
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615 **Figures**

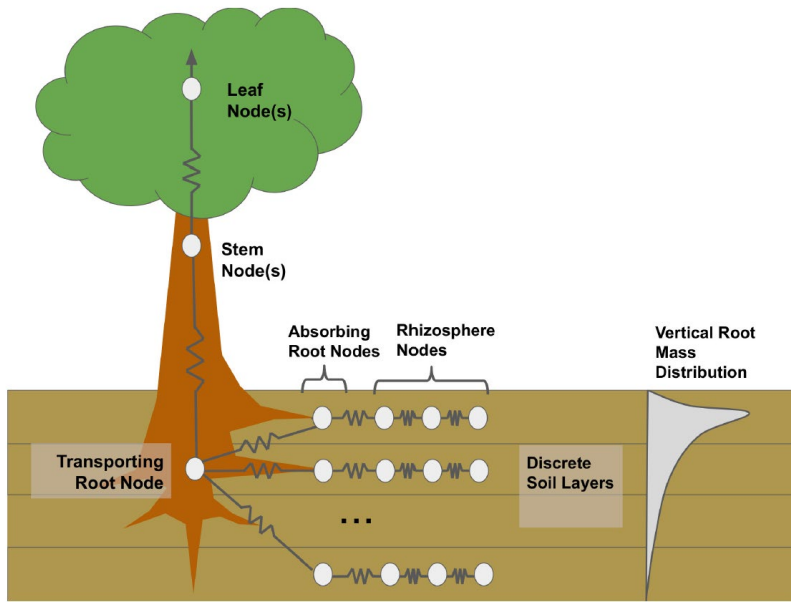
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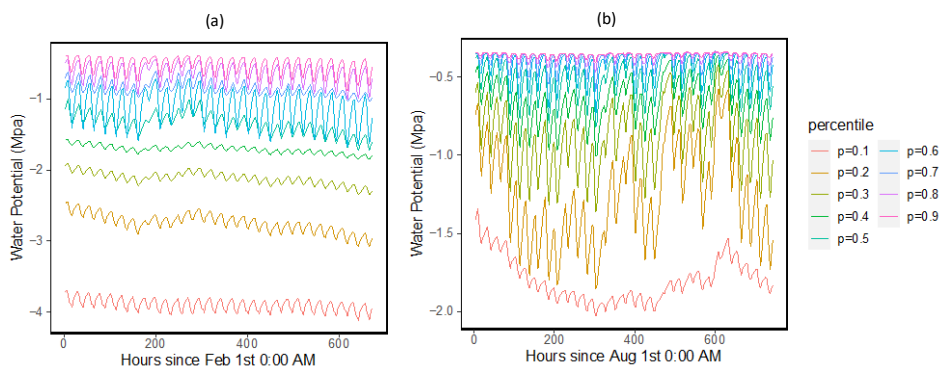


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620 **Figure 1: Diagram of FATES-HYDO with simulation of rhizosphere shell, absorbing roots, transporting roots, stem and**
 621 **leaves. The model is solved for different soil layers with different root distributions.**

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626 **Figure 2:** Simulated ranges of leaf water potential for February (a) and August (a), 2016 **for trees with DBH > 60cm**. The
627 percentiles are calculated based on the monthly mean values of leaf water potentials for the 1000 ensemble simulations.

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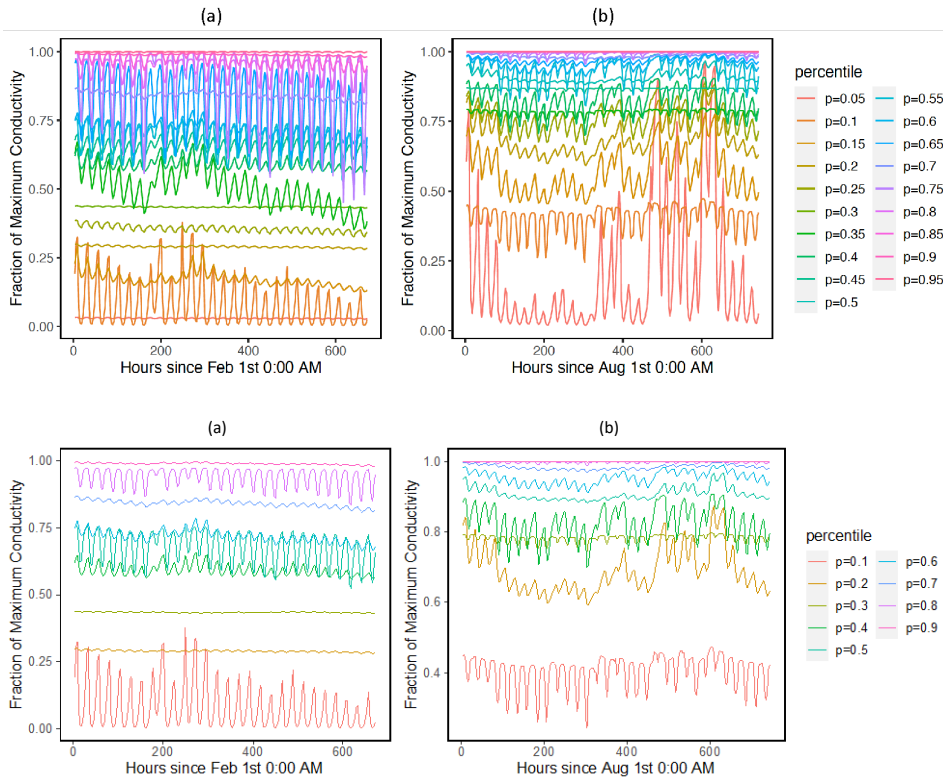
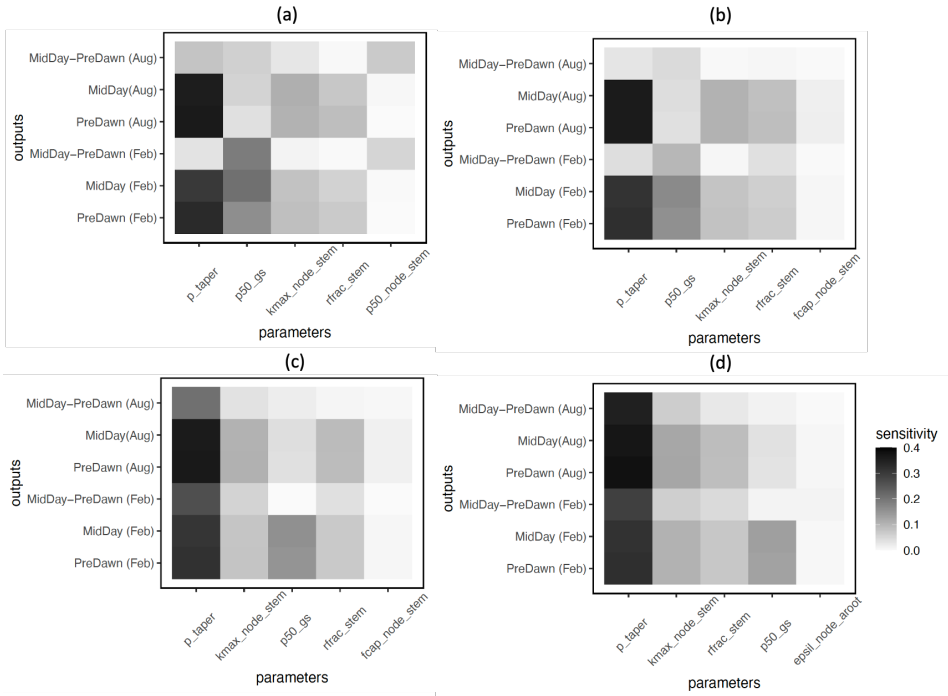
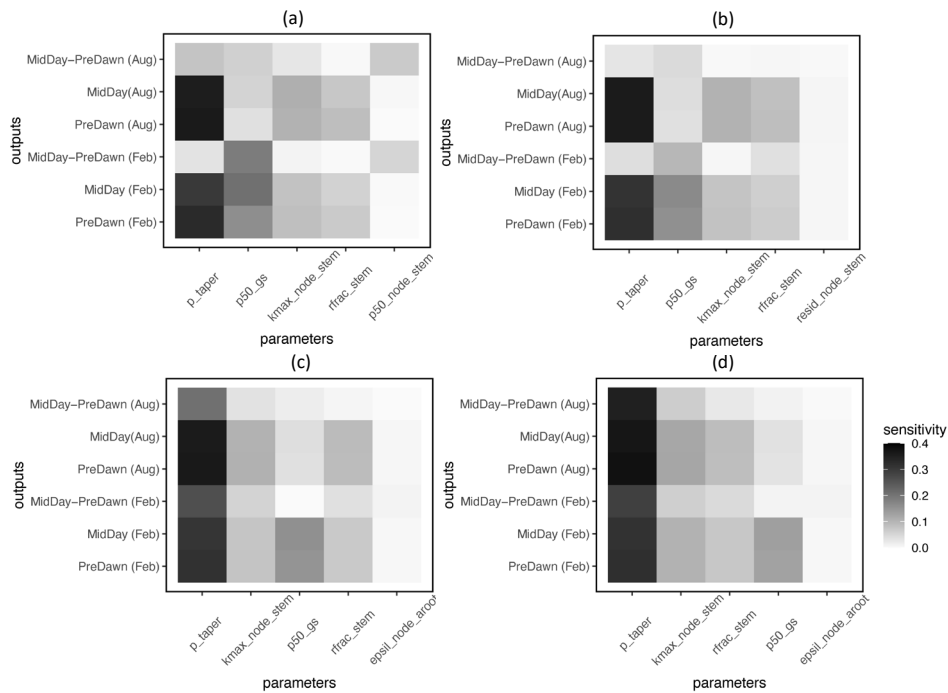


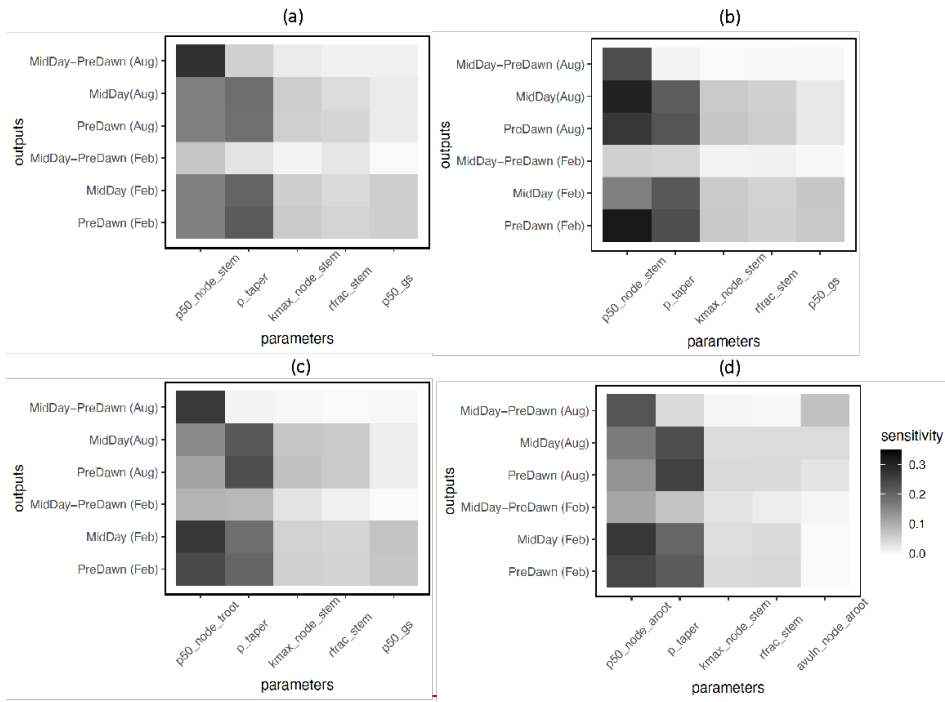
Figure 23: Simulated ranges of fraction of maximum hydraulic conductivity of stem for February (a) and August (a), 2016- for trees with DBH > 60cm. The percentiles are calculated based on the monthly mean values of leaf water potentials for the 1000 ensemble simulations.



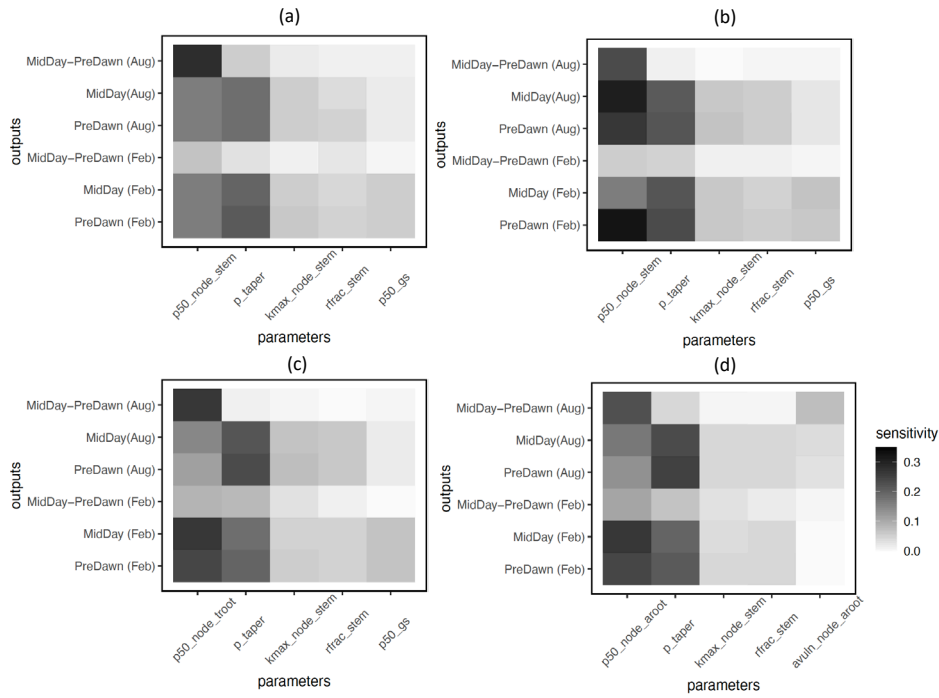


638
 639 **Figure 34:** Key parameters that control simulated water potentials for leaf (a), stem (b), transporting root (c) and
 640 **absorbing root (d), for trees with DBH > 60cm.** The sensitivity value refers to the proportion of total model output variance
 641 contributed by a specific parameter (0-1). See Table 1 for the explanation of the parameters.

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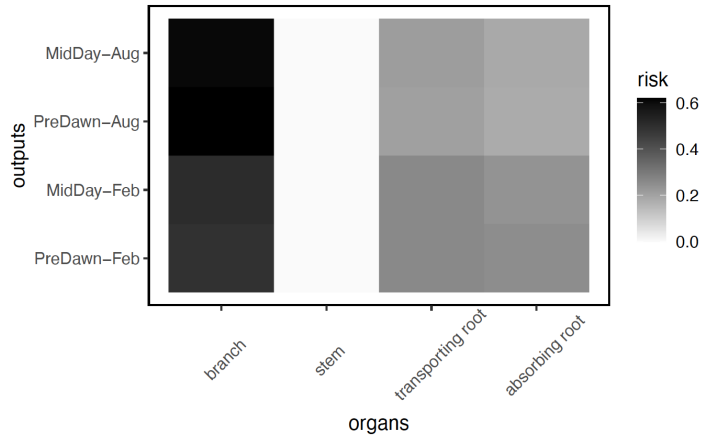


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647 **Figure 45:** Key parameters that control simulated loss of conductivity for branch (a), stem (b), transporting root (c) and
648 absorbing root (d-), for trees with DBH > 60cm. The sensitivity value refers to the proportion of total model output variance
649 contributed by a specific parameter. See Table 1 for the explanation of the parameters. See Table 1 for the description of
650 parameters.

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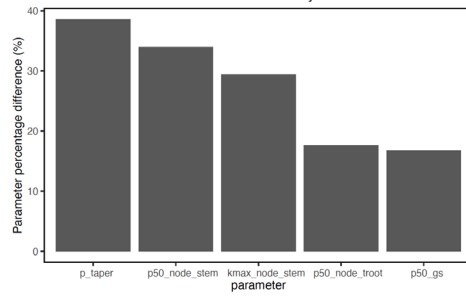
653 **Figure 56:** Risk on the continuum for hydraulic failure as measured by percentage of total number of simulations with
 654 highest loss of conductivity for a specific organ (branch, stem, transporting root and absorbing root), **for trees with DBH**
 655 **> 60cm.** As the model does not specifically simulate the branch, we calculated the risk of loss of conductivity based on the leaf
 656 water potential and hydraulic vulnerability curve from xylem.

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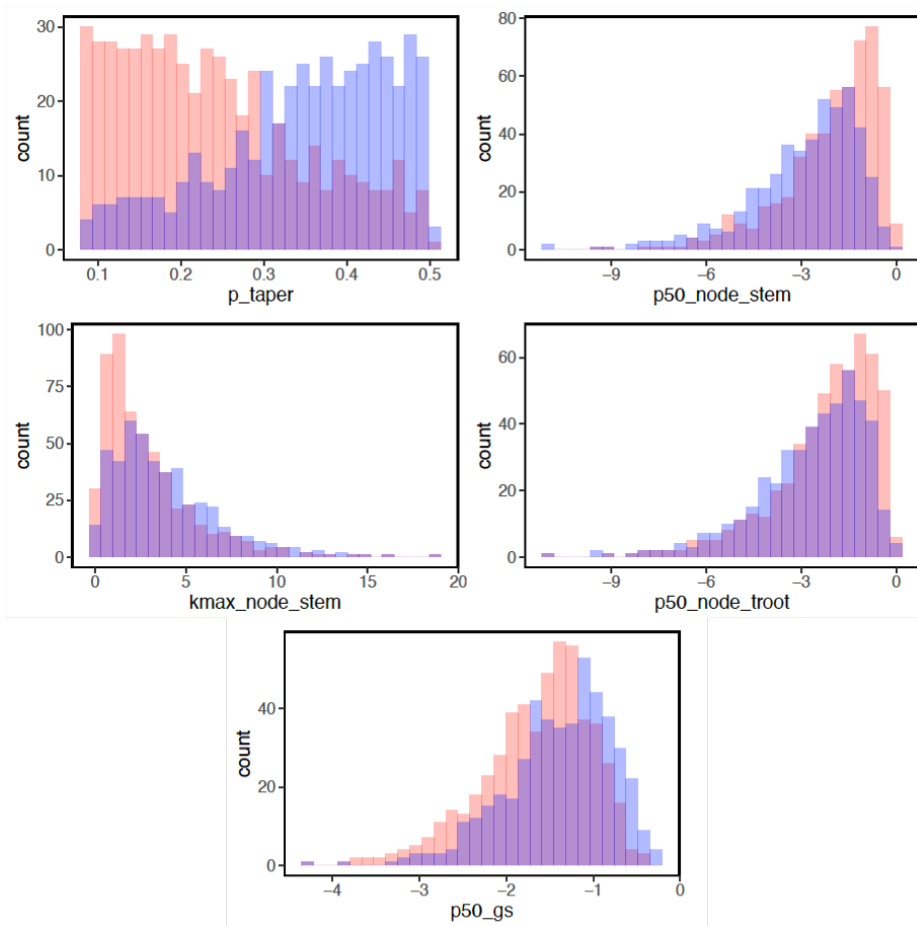


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662 **Figure 67:** Mean trait percentage difference for model ensemble simulations with loss of hydraulic conductivity larger
663 than 50% and ensemble simulations with loss of hydraulic conductivity less than 50%, for trees with DBH > 60cm. See
664 Table 1 for the description of parameters.

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 668 **Figure 78:** Parameter difference for ensemble members with risk of mortality, **for trees with DBH > 60cm**. Blue bars
 669 indicate parameter values with lower mortality risk (<50% loss of hydraulic conductivity). Red bars indicate parameter values
 670 with higher mortality risk (>= 50% loss of hydraulic conductivity) and purple bars indicate parameter values stacked from
 671 transparent red/blue bars. See Table 1 for the description of parameters.

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PARAMETER (EQUATION NUMBER)	SYMBOL	UNITS	DISTRIBUTION ¹	SOURCES & NOTES
Pressure-Volume (PV) curve (water content – water potential relationship)				
saturated water content (thetas_node) (Eq. 5)	$\theta_{sat,x}$	cm ³ cm ⁻³	Leaf: Beta (9.69, 6.20) Stem: Beta (12.67, 7.4626) TRoot and AROOT: Beta (22.98, 5.29)	Christoffersen et al. (2016) Iversen et al. (2017) Wright et al. (2010) Roderick et al. (1999) Sack et al. (2003) Binks et al. (2016)
turgor loss point (tlp_node) (Eq. 5)	π_{tlp}	MPa	$\pi_{tlp} = \frac{(\pi_0 \varepsilon)}{(\pi_0 + \varepsilon)}$	Bartlett et al. (2012, 2014) $\pi_{tlp} = \frac{(\pi_0 \varepsilon)}{(\pi_0 + \varepsilon)}$
osmotic potential at full turgor (pinot_node) (Eq. 6)	π_0	MPa	Leaf: G [9.8, 6.26], Stem, TRoot, ARoot: LN [0.32, 0.39]	Bartlett et al. (2012, 2014, 2016) and Christoffersen et al. (2016)
bulk elastic modulus (epsil_node) (Eq. 7)	ε	MPa	Leaf: G (4.07, 4.12) Stem, TRoot and ARoot: G [3.57, 3.84]	Bartlett et al. (2012, 2014), and Christoffersen et al. (2016)
residual water fraction (resid_node) (Eq. 5)	RWC_r	unitless	Leaf: B [2.14, 4.10] Stem, TRoot and ARoot: B [2.71, 4.53]	Bartlett et al. (2012, 2014), Christoffersen et al. (2016)
fraction of water in capillary reserve (fcap_node)	f_{cap}	unitless	U [0.1, 0.7]	Christoffersen et al. (2016)
VULNERABILITY CURVE (WATER POTENTIAL – HYDRAULIC CONDUCTIVITY RELATIONSHIP)				
water potential at 50% loss of max conductivity (p50_node) (Eq. 3)	$P_{50,x}$	MPa	Stem, TRoot and ARoot: G [2.07, 1.18]	Choat et al. (2012)
vulnerability curve shape parameter (avuln_node) (Eq. 3)	α_x	unitless	Stem, TRoot and ARoot: LN [0.82, 0.66]	Choat et al. (2012)

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xylem conductivity per unit sapwood area ($k_{max_node_stem}$) (Eq. 7)	$k_{s,max}$	kg m ⁻¹ s ⁻¹ MPa ⁻¹	G [1.41, 2.37]	Choat et al. (2012)
Leaf hydraulics				
leaf water potential at 50% loss of max gs (p_{50_gs}) (Eq. 11)	$P_{50,gs}$	MPa	G [5.73, 0.27]	Klein (2014)
stomatal vulnerability shape parameter (a_{gs}) (Eq. 11)	a_{gs}	unitless	$a_{gs} = -2.406 P_{50,gs} (-P_{50,gs})^{-1.25}$	Christoffersen et al. (2016); derived according to empirical equation: $a_{gs} = -2.406 P_{50,gs} (-P_{50,gs})^{-1.25}$
Leaf cuticular conductivity (k_{0_leaf}) (Eq. 10)	$k_{cut} g_0$	umol m ⁻² s ⁻¹	LN [1.04, 0.84]	This study, based on (M. Slot, unpublished data measured by Martijn Slot)
Plant Hydraulic Architecture				
Xylem taper exponent for sapwood (p_taper) (Eq. 8)	p	(-)	U (0.08, 0.5)	Savage et al. (2010)
Leaf area to sapwood area ratio (la_{2sa}) (Eq. 7)	$la_{2sa} \frac{A_l}{A_s}$	(-)	LN (-0.48, 0.77)	Choat et al. (2012)
Root hydraulic Traits				
specific root length (srl) (Eq. 12)	srl	m g ⁻¹	G [1.70, 35.31]	Iversen et al. (2017)
absorbing root radius (rs_2) (Eq. 12)	r	mm	LN [-1.91, 0.79]	Iversen et al. (2017)
fraction of total tree resistance that is aboveground ($rfrac_stem$) (Eq. 9)	$rfrac_{rac,stem}$	Unitless	U [0.1, 0.7]	This study; empirical
root-soil interface conductivity per unit surface area ($Kr1$) (Eq. 13)	$k_{r1,max}$	kg m ⁻¹ s ⁻¹ MPa ⁻¹	G [1.41, 2.37]	This study; empirically set the same as xylem conductivity
maximum root water loss rate ($Kr2$) (Eq. 13)	$k_{r2,max}$	kg m ⁻¹ s ⁻¹ MPa ⁻¹	LN [-6.80, 0.92]	Wolfe (2020); Empirically set as 1/1000 bark water loss rate

676 **Note:** 1:Beta distribution; U- Uniform distribution [lower limit, upper limit]; N-Gaussian distribution

677 (mean, standard deviation); LN-Log Normal Distribution [mean, standard deviation]; G-Gamma

678 distribution (lambda, scale); TRoot-Transporting root; ARoot-Absorbing root.

679

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680 Reference

681 ~~1.~~ Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhausser, S. M.,
682 Tissue, D. T., Huxman, T. E., Hudson, P. J., Franz, T. E., Allen, C. D., Anderegg, L. D. L.,
683 Barron-Gafford, G. A., Beerling, D. J., Breshears, D. D., Brodrribb, T. J., Bugmann, H., Cobb, R.
684 C., Collins, A. D., Dickman, L. T., Duan, H. L., Ewers, B. E., Galiano, L., Galvez, D. A., Garcia-
685 Forner, N., Gaylord, M. L., Germino, M. J., Gessler, A., Hacke, U. G., Hakamada, R., Hector,
686 A., Jenkins, M. W., Kane, J. M., Kolb, T. E., Law, D. J., Lewis, J. D., Limousin, J. M., Love, D.
687 M., Macalady, A. K., Martinez-Vilalta, J., Mencuccini, M., Mitchell, P. J., Muss, J. D., O'Brien,
688 M. J., O'Grady, A. P., Pangle, R. E., Pinkard, E. A., Piper, F. I., Plaut, J. A., Pockman, W. T.,
689 Quirk, J., Reinhardt, K., Ripullone, F., Ryan, M. G., Sala, A., Sevanto, S., Sperry, J. S., Vargas,
690 R., Vennetier, M., Way, D. A., Xu, C. G., Yepez, E. A., and McDowell, N. G.: A multi-species
691 synthesis of physiological mechanisms in drought-induced tree mortality, *Nat Ecol Evol*, 1,
692 1285-1291, 10.1038/s41559-017-0248-x, 2017.

693 ~~2.~~ Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., and
694 Jansen, S.: Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-
695 induced tree mortality across the globe, *P Natl Acad Sci USA*, 113, 5024-5029,
696 10.1073/pnas.1525678113, 2016.

697 ~~3.~~ Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K. L., Bowling, D. R.,
698 Gabbitas, R., Karp, D. S., Pacala, S., Sperry, J. S., Sulman, B. N., and Zenes, N.: Hydraulic
699 diversity of forests regulates ecosystem resilience during drought, *Nature*, 561, 538-541,
700 10.1038/s41586-018-0539-7, 2018.

701 ~~4.~~ Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein,
702 P., Schwinger, J., Bopp, L., Boucher, O., Cadule, P., Chamberlain, M. A., Christian, J. R., Delire,
703 C., Fisher, R. A., Hajima, T., Ilyina, T., Joetzjer, E., Kawamiya, M., Koven, C. D., Krasting, J.
704 P., Law, R. M., Lawrence, D. M., Lenton, A., Lindsay, K., Pongratz, J., Raddatz, T., Seferian,
705 R., Tachiiri, K., Tjiputra, J. F., Wiltshire, A., Wu, T. W., and Ziehn, T.: Carbon-concentration
706 and carbon-climate feedbacks in CMIP6 models and their comparison to CMIP5 models,
707 *Biogeosciences*, 17, 4173-4222, 10.5194/bg-17-4173-2020, 2020.

708 ~~5.~~ Bartlett, M. K., ~~Detto, M., and Pacala, S. W.: Predicting shifts in the functional~~
709 ~~composition of tropical forests under increased drought and CO2 from trade-offs among~~
710 ~~plant hydraulic traits, *Ecol Lett*, 22, 67-77, 10.1111/ele.13168, 2019.~~

711 ~~6.~~ Bartlett, M. K., Scoffoni, C., and Sack, L.: The determinants of leaf turgor loss point and
712 prediction of drought tolerance of species and biomes: a global meta-analysis, *Ecol Lett*, 15, 393-
713 405, 10.1111/j.1461-0248.2012.01751.x, 2012.

714 ~~7.~~ Bartlett, M. K., Klein, T., Jansen, S., Choat, B., and Sack, L.: The correlations and
715 sequence of plant stomatal, hydraulic, and wilting responses to drought, *P Natl Acad Sci USA*,
716 113, 13098-13103, 10.1073/pnas.1604088113, 2016.

717 ~~8.~~ Bartlett, M. K., Zhang, Y., Kreidler, N., Sun, S. W., Ardy, R., Cao, K. F., and Sack, L.:
718 Global analysis of plasticity in turgor loss point, a key drought tolerance trait, *Ecol Lett*, 17,
719 1580-1590, 10.1111/ele.12374, 2014.

720 ~~Bennett, A. C., McDowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J.: Larger trees suffer~~
721 ~~most during drought in forests worldwide, *Nat Plants*, 1, Artn 15139~~
722 ~~10.1038/Nplants.2015.139, 2015.~~

723 ~~9.~~ Berenguer, E., Lennox, G. D., Ferreira, J., Malhi, Y., Aragao, L. E. O. C., Barreto, J. R.,
724 Espirito-Santo, F. D., Figueiredo, A. E. S., Franca, F., Gardner, T. A., Joly, C. A., Palmeira, A.

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725 F., Quesada, C. A., Rossi, L. C., de Seixas, M. M. M., Smith, C. C., Withey, K., and Barlow, J.:

726 Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests, *P Natl*

727 *Acad Sci USA*, 118, ARTN e2019377118: 10.1073/pnas.2019377118, 2021.

728 [Bhagat, N., Raghav, M., Dubey, S., and Bedi, N.: Bacterial Exopolysaccharides: Insight into](#)

729 [Their Role in Plant Abiotic Stress Tolerance, *J Microbiol Biotechn*, 31, 1045-1059,](#)

730 [10.4014/jmb.2105.05009, 2021.](#)

731 ~~40.~~ Binks, O., Meir, P., Rowland, L., da Costa, A. C. L., Vasconcelos, S. S., de Oliveira, A.

732 A. R., Ferreira, L., Christoffersen, B., Nardini, A., and Mencuccini, M.: Plasticity in leaf-level

733 water relations of tropical rainforest trees in response to experimental drought, *New Phytol*, 211,

734 477-488, 10.1111/nph.13927, 2016.

735 ~~41.~~ Bonal, D., Burban, B., Stahl, C., Wagner, F., and Hérault, B.: The response of tropical

736 rainforests to drought-lessons from recent research and future prospects, *Ann Forest Sci*, 73, 27-

737 44, 10.1007/s13595-015-0522-5, 2016.

738 ~~42.~~ Bonan, G. B.: Forests and climate change: Forcings, feedbacks, and the climate benefits

739 of forests, *Science*, 320, 1444-1449, 10.1126/science.1155121, 2008.

740 ~~43.~~ Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J. A., Mozzherin, D., Rees, T., Matasci,

741 N., Narro, M. L., Piel, W. H., and McKay, S. J.: The taxonomic name resolution service: an

742 online tool for automated standardization of plant names, *BMC bioinformatics*, 14, 1-15, 2013.

743 ~~44.~~ Breshears, D. D., Myers, O. B., Meyer, C. W., Barnes, F. J., Zou, C. B., Allen, C. D.,

744 McDowell, N. G., and Pockman, W. T.: Tree die-off in response to global change-type drought:

745 mortality insights from a decade of plant water potential measurements, *Front Ecol Environ*, 7,

746 185-189, 10.1890/080016, 2009.

747 ~~45.~~ Caldwell, P. M., Mametjanov, A., Tang, Q., Van Roekel, L. P., Golaz, J. C., Lin, W. Y.,

748 Bader, D. C., Keen, N. D., Feng, Y., Jacob, R., Maltrud, M. E., Roberts, A. F., Taylor, M. A.,

749 Veneziani, M., Wang, H. L., Wolfe, J. D., Balaguru, K., Cameron-Smith, P., Dong, L., Klein, S.

750 A., Leung, L. R., Li, H. Y., Li, Q., Liu, X. H., Neale, R. B., Pinheiro, M., Qian, Y., Ullrich, P.

751 A., Xie, S. C., Yang, Y., Zhang, Y. Y., Zhang, K., and Zhou, T.: The DOE E3SM Coupled

752 Model Version 1: Description and Results at High Resolution, *J Adv Model Earth Sy*, 11, 4095-

753 4146, 10.1029/2019ms001870, 2019.

754 ~~46.~~ Chen, J. W., Zhang, Q., Li, X. S., and Cao, K. F.: Independence of stem and leaf

755 hydraulic traits in six Euphorbiaceae tree species with contrasting leaf phenology, *Planta*, 230,

756 459-468, 10.1007/s00425-009-0959-6, 2009.

757 ~~47.~~ Chitra-Tarak, R., Xu, C. G., Aguilar, S., Anderson-Teixeira, K. J., Chambers, J., Detto,

758 M., Faybishenko, B., Fisher, R. A., Knox, R. G., Koven, C. D., Kueppers, L. M., Kunert, N.,

759 Kupers, S. J., McDowell, N. G., Newman, B. D., Paton, S. R., Perez, R., Ruiz, L., Sack, L.,

760 Warren, J. M., Wolfe, B. T., Wright, C., Wright, S. J., Zailaa, J., and McMahon, S. M.:

761 Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest,

762 *New Phytol*, 231, 1798-1813, 10.1111/nph.17464, 2021.

763 ~~48.~~ Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J.,

764 Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martinez-

765 Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., Pratt, R. B.,

766 Sperry, J. S., Westoby, M., Wright, I. J., and Zanne, A. E.: Global convergence in the

767 vulnerability of forests to drought, *Nature*, 491, 752+, 10.1038/nature11688, 2012.

768 ~~49.~~ Christoffersen, B. O., Gloor, M., Fauset, S., Fyllas, N. M., Galbraith, D. R., Baker, T. R.,

769 Kruijt, B., Rowland, L., Fisher, R. A., Binks, O. J., Sevanto, S., Xu, C. G., Jansen, S., Choat, B.,

770 Mencuccini, M., McDowell, N. G., and Meir, P.: Linking hydraulic traits to tropical forest

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771 function in a size-structured and trait-driven model (TFS v.1-Hydro), *Geosci Model Dev*, 9,
772 4227-4255, 10.5194/gmd-9-4227-2016, 2016.

773 [Dichio, B., Xiloyannis, C., Sofo, A., and Montanaro, G.: Osmotic regulation in leaves and roots](#)
774 [of olive trees during a water deficit and rewatering, *Tree Physiol*, 26, 179-185, DOI](#)
775 [10.1093/treephys/26.2.179, 2006.](#)

776 [Fang, Y. L., Leung, L. R., Knox, R., Koven, C., and Bond-Lamberty, B.: Impact of the numerical](#)
777 [solution approach of a plant hydrodynamic model \(v0.1\) on vegetation dynamics, *Geosci Model*](#)
778 [Dev, 15, 6385-6398, 10.5194/gmd-15-6385-2022, 2022.](#)

779 ~~20.~~ Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C.,
780 Meir, P., and Woodward, F. I.: Assessing uncertainties in a second-generation dynamic
781 vegetation model caused by ecological scale limitations, *New Phytol*, 187, 666-681,
782 10.1111/j.1469-8137.2010.03340.x, 2010.

783 ~~24.~~ Fisher, R. A. and Koven, C. D.: Perspectives on the Future of Land Surface Models and
784 the Challenges of Representing Complex Terrestrial Systems, *J Adv Model Earth Sy*, 12, ARTN
785 e2018MS001453: 10.1029/2018MS001453, 2020.

786 ~~22.~~ Fisher, R. A., Muszala, S., Versteinstein, M., Lawrence, P., Xu, C., McDowell, N. G.,
787 Knox, R. G., Koven, C., Holm, J., Rogers, B. M., Spessa, A., Lawrence, D., and Bonan, G.:
788 Taking off the training wheels: the properties of a dynamic vegetation model without climate
789 envelopes, *CLM4.5(ED)*, *Geosci Model Dev*, 8, 3593-3619, 10.5194/gmd-8-3593-2015, 2015.

790 ~~23.~~ Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C.,
791 Farrior, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo,
792 M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H.,
793 Shuman, J. K., Smith, B., Trugman, A. T., Viskari, T., Verbeeck, H., Weng, E. S., Xu, C. G., Xu,
794 X. T., Zhang, T., and Moorcroft, P. R.: Vegetation demographics in Earth System Models: A
795 review of progress and priorities, *Global Change Biol*, 24, 35-54, 10.1111/gcb.13910, 2018.

796 ~~24.~~ Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G., Pratt, R. B., Bhaskar,
797 R., Brodribb, T. J., Bucci, S. J., Cao, K. F., Cochard, H., Delzon, S., Domec, J. C., Fan, Z. X.,
798 Feild, T. S., Jacobsen, A. L., Johnson, D. M., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr,
799 S., McCulloh, K. A., Mencuccini, M., Mitchell, P. J., Morris, H., Nardini, A., Pittermann, J.,
800 Plavcova, L., Schreiber, S. G., Sperry, J. S., Wright, I. J., and Zanne, A. E.: Weak tradeoff
801 between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant
802 species, *New Phytol*, 209, 123-136, 10.1111/nph.13646, 2016.

803 [Hammond, W. M., Yu, K., Wilson, L. A., Will, R. E., Anderegg, W. R. L., and Adams, H. D.:](#)
804 [Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree](#)
805 [mortality, *New Phytol*, 223, 1834-1843, <https://doi.org/10.1111/nph.15922>, 2019.](#)

806 ~~25.~~ Hochberg, U., Rockwell, F. E., Holbrook, N. M., and Cochard, H.: Iso/Anisohydry: A
807 Plant-Environment Interaction Rather Than a Simple Hydraulic Trait, *Trends Plant Sci*, 23, 112-
808 120, 10.1016/j.tplants.2017.11.002, 2018.

809 ~~26.~~ Huang, M. Y., Xu, Y., Longo, M., Keller, M., Knox, R. G., Koven, C. D., and Fisher, R.
810 A.: Assessing impacts of selective logging on water, energy, and carbon budgets and ecosystem
811 dynamics in Amazon forests using the Functionally Assembled Terrestrial Ecosystem Simulator,
812 *Biogeosciences*, 17, 4999-5023, 10.5194/bg-17-4999-2020, 2020.

813 ~~27.~~ Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T.,
814 Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., van
815 Bodegom, P. M., and Violle, C.: A global Fine-Root Ecology Database to address below-ground
816 challenges in plant ecology, *New Phytol*, 215, 15-26, 10.1111/nph.14486, 2017.

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§17 ~~28.~~ Kennedy, D., Swenson, S., Oleson, K. W., Lawrence, D. M., Fisher, R., da Costa, A. C.
 818 L., and Gentine, P.: Implementing Plant Hydraulics in the Community Land Model, Version 5, J
 819 Adv Model Earth Sy, 11, 485-513, 10.1029/2018ms001500, 2019.
 §20 ~~29.~~ Klein, T.: The variability of stomatal sensitivity to leaf water potential across tree species
 821 indicates a continuum between isohydric and anisohydric behaviours, Funct Ecol, 28, 1313-
 822 1320, 10.1111/1365-2435.12289, 2014.
 §23 ~~30.~~ Koven, C. D., Knox, R. G., Fisher, R. A., Chambers, J. Q., Christoffersen, B. O., Davies,
 824 S. J., Detto, M., Dietze, M. C., Faybishenko, B., Holm, J., Huang, M. Y., Kovenock, M.,
 825 Kueppers, L. M., Lemieux, G., Massoud, E., McDowel, N. G., Muller-Landau, H. C., Needham,
 826 J. F., Norby, R. J., Powell, T., Rogers, A., Serbin, S. P., Shuman, J. K., Swann, A. L. S.,
 827 Varadharajan, C., Walker, A. P., Wright, S. J., and Xu, C. G.: Benchmarking and parameter
 828 sensitivity of physiological and vegetation dynamics using the Functionally Assembled
 829 Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama, Biogeosciences,
 830 17, 3017-3044, 10.5194/bg-17-3017-2020, 2020.
 §31 ~~31.~~ Kunert, N., Zailaa, J., Herrmann, V., Muller-Landau, H. C., Wright, S. J., Perez, R.,
 832 McMahon, S. M., Condit, R. C., Hubbell, S. P., Sack, L., Davies, S. J., and Anderson-Teixeira,
 833 K. J.: Leaf turgor loss point shapes local and regional distributions of evergreen but not
 834 deciduous tropical trees, New Phytol, 230, 485-496, 10.1111/nph.17187, 2021.
 §35 ~~32.~~ Kursar, T. A., Engelbrecht, B. M. J., Burke, A., Tyree, M. T., El Omari, B., and Giraldo,
 836 J. P.: Tolerance to low leaf water status of tropical tree seedlings is related to drought
 837 performance and distribution, Funct Ecol, 23, 93-102, 10.1111/j.1365-2435.2008.01483.x, 2009.
 §38 ~~Lambert, M. S. A., Tang, H., Aas, K. S., Stordal, F., Fisher, R. A., Fang, Y. L., Ding, J. Y., and~~
 839 ~~Parmentier, F. J. W.: Inclusion of a cold hardening scheme to represent frost tolerance is~~
 840 ~~essential to model realistic plant hydraulics in the Arctic-boreal zone in CLM5.0-FATES-Hydro,~~
 841 ~~Geosci Model Dev, 15, 8809-8829, 10.5194/gmd-15-8809-2022, 2022.~~
 842 ~~Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G.,~~
 843 ~~Collier, N., Ghimire, B., van Kampenhout, L., Kennedy, D., Kluzek, E., Lawrence, P. J., Li, F.,~~
 844 ~~Li, H. Y., Lombardozzi, D., Riley, W. J., Sacks, W. J., Shi, M. J., Vertenstein, M., Wieder, W.~~
 845 ~~R., Xu, C. G., Ali, A. A., Badger, A. M., Bisht, G., van den Broeke, M., Brunke, M. A., Burns, S.~~
 846 ~~P., Buzan, J., Clark, M., Craig, A., Dahlin, K., Drewniak, B., Fisher, J. B., Flanner, M., Fox, A.~~
 847 ~~M., Gentine, P., Hoffman, F., Keppel-Aleks, G., Knox, R., Kumar, S., Lenaerts, J., Leung, L. R.,~~
 848 ~~Lipscomb, W. H., Lu, Y. Q., Pandey, A., Pelletier, J. D., Perket, J., Randerson, J. T., Ricciuto, D.~~
 849 ~~M., Sanderson, B. M., Slater, A., Subin, Z. M., Tang, J. Y., Thomas, R. Q., Martin, M. V., and~~
 850 ~~Zeng, X. B.: The Community Land Model Version 5: Description of New Features,~~
 851 ~~Benchmarking, and Impact of Forcing Uncertainty, J Adv Model Earth Sy, 11, 4245-4287,~~
 852 ~~10.1029/2018ms001583, 2019.~~
 §53 ~~33.~~ Manzoni, S., Vico, G., Katul, G., Palmroth, S., Jackson, R. B., and Porporato, A.:
 854 Hydraulic limits on maximum plant transpiration and the emergence of the safety-efficiency
 855 trade-off, New Phytol, 198, 169-178, 10.1111/nph.12126, 2013.
 §56 ~~34.~~ Massoud, E. C., Xu, C. G., Fisher, R. A., Knox, R. G., Walker, A. P., Serbin, S. P.,
 857 Christoffersen, B. O., Holm, J. A., Kueppers, L. M., Ricciuto, D. M., Wei, L., Johnson, D. J.,
 858 Chambers, J. Q., Koven, C. D., McDowell, N. G., and Vrugt, J. A.: Identification of key
 859 parameters controlling demographically structured vegetation dynamics in a land surface model:
 860 CLM4.5(FATES), Geosci Model Dev, 12, 4133-4164, 10.5194/gmd-12-4133-2019, 2019.
 §61 ~~35.~~ McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brien, R., Chambers,
 862 J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher, R., Fontes,

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863 C. G., Galbraith, D., Goodsman, D., Grossiord, C., Hartmann, H., Holm, J., Johnson, D. J.,
864 Kassim, A., Keller, M., Koven, C., Kueppers, L., Kumagai, T., Malhi, Y., McMahon, S. M.,
865 Mencuccini, M., Meir, P., Moorcroft, P., Muller-Landau, H. C., Phillips, O. L., Powell, T.,
866 Sierra, C. A., Sperry, J., Warren, J., Xu, C. G., and Xu, X. T.: Drivers and mechanisms of tree
867 mortality in moist tropical forests, *New Phytol*, 219, 851-869, 10.1111/nph.15027, 2018.
868 McDowell, N. G., [Fisher, R. A., Xu, C. G., Domec, J. C., Holtta, T., Mackay, D. S., Sperry, J. S.,](#)
869 [Boutz, A., Dickman, L., Gehres, N., Limousin, J. M., Macalady, A., Martinez-Vilalta, J.,](#)
870 [Mencuccini, M., Plaut, J. A., Ogee, J., Pangle, R. E., Rasse, D. P., Ryan, M. G., Sevanto, S.,](#)
871 [Waring, R. H., Williams, A. P., Yopez, E. A., and Pockman, W. T.:](#) Evaluating theories of
872 drought-induced vegetation mortality using a multimodel-experiment framework, *New Phytol*,
873 200, 304-321, 10.1111/nph.12465, 2013.
874 36. [McDowell, N. G., Sapes, G., Pivovarov, A., Adams, H. D., Allen, C. D., Anderegg, W.](#)
875 [R. L., Arend, M., Breshears, D. D., Brodrigg, T., Choat, B., Cochard, H., De Caceres, M., De](#)
876 [Kauwe, M. G., Grossiord, C., Hammond, W. M., Hartmann, H., Hoch, G., Kahmen, A., Klein,](#)
877 [T., Mackay, D. S., Mantova, M., Martinez-Vilalta, J., Medlyn, B. E., Mencuccini, M., Nardini,](#)
878 [A., Oliveira, R. S., Sala, A., Tissue, D. T., Torres-Ruiz, J. M., Trowbridge, A. M., Trugman, A.](#)
879 [T., Wiley, E., and Xu, C. G.:](#) Mechanisms of woody-plant mortality under rising drought, CO₂
880 and vapour pressure deficit, *Nat Rev Earth Env*, 3, 294-308, 10.1038/s43017-022-00272-1, 2022.
881 37. Moorcroft, P. R., Hurtt, G. C., and Pacala, S. W.: A method for scaling vegetation
882 dynamics: The ecosystem demography model (ED), *Ecol Monogr*, 71, 557-585, 10.1890/0012-
883 9615(2001)071[0557:Amfsvd]2.0.Co;2, 2001.
884 38. Needham, J. F., Chambers, J., Fisher, R., Knox, R., and Koven, C. D.: Forest responses to
885 simulated elevated CO₂ under alternate hypotheses of size- and age-dependent mortality, *Global*
886 *Change Biol*, 26, 5734-5753, 10.1111/gcb.15254, 2020.
887 [Norman, J.:](#) *Modelling the complete crop canopy, in Modification of the Aerial Environment of*
888 *Plants, Am. Soc. Agri. Eng. Monograph*, 2, 249-277, 1979.
889 [North, G. B. and Nobel, P. S.:](#) *Drought-Induced Changes in Hydraulic Conductivity and*
890 *Structure in Roots of Ferocactus-Acanthodes and Opuntia-Ficus-Indica, New Phytol.* 120, 9-19,
891 DOI 10.1111/j.1469-8137.1992.tb01053.x, 1992.
892 [Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis,](#)
893 [S., Li, F., Riley, W. J., Subin, Z. M., Swenson, S. C., Thornton, P. E., Bozbiyik, A., Fisher, R.,](#)
894 [Heald, C. L., Kluzek, E., Lamarque, J.-F., Lawrence, P. J., Leung, L. R., Lipscomb, W.,](#)
895 [Muszala, S., Ricciuto, D. M., Sacks, W., Sun, Y., Tang, J., & Yang, Z.-L.:](#) Technical description
896 of version 4.5 of the Community Land Model (CLM) National Center for Atmospheric Research,
897 Boulder, Colorado, USA. Tech. Rep. NCAR/TN-503+STR, 2013.
898 [Olson, M. E., Anfodillo, T., Gleason, S. M., and McCulloh, K. A.:](#) Tip-to-base xylem conduit
899 widening as an adaptation: causes, consequences, and empirical priorities, *New Phytol*, 229,
900 1877-1893, 10.1111/nph.16961, 2021.
901 39. Paton, S.: Yearly Reports Barro Colorado Island, Smithsonian Tropical Research
902 Institute, <https://doi.org/10.25573/data.11799111.v3><https://doi.org/10.25573/data.11799111.v3>,
903 2020.
904 40. Pineda-Garcia, F., Paz, H., and Meinzer, F. C.: Drought resistance in early and late
905 secondary successional species from a tropical dry forest: the interplay between xylem resistance
906 to embolism, sapwood water storage and leaf shedding, *Plant Cell Environ*, 36, 405-418,
907 10.1111/j.1365-3040.2012.02582.x, 2013.

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908 [Poudel, M., Mendes, R., Costa, L. A., Bueno, C. G., Meng, Y., Folimonova, S. Y., Garrett, K.](#)
909 [A., and Martins, S. J.: The role of plant-associated bacteria, fungi, and viruses in drought stress](#)
910 [mitigation. *Frontiers in microbiology*, 12, 3058, 2021.](#)
911 ~~41.~~ Powell, T. L., Wheeler, J. K., de Oliveira, A. A. R., da Costa, A. C. L., Saleska, S. R.,
912 Meir, P., and Moorcroft, P. R.: Differences in xylem and leaf hydraulic traits explain differences
913 in drought tolerance among mature Amazon rainforest trees, *Global Change Biol*, 23, 4280-4293,
914 10.1111/gcb.13731, 2017.
915 ~~42.~~ Powell, T. L., Koven, C. D., Johnson, D. J., Faybishenko, B., Fisher, R. A., Knox, R. G.,
916 McDowell, N. G., Condit, R., Hubbell, S. P., Wright, S. J., Chambers, J. Q., and Kueppers, L.
917 M.: Variation in hydroclimate sustains tropical forest biomass and promotes functional diversity,
918 *New Phytol*, 219, 932-946, 10.1111/nph.15271, 2018.
919 ~~43.~~ Roderick, M. L., Berry, S. L., Saunders, A. R., and Noble, I. R.: On the relationship
920 between the composition, morphology and function of leaves, *Funct Ecol*, 13, 696-710, DOI
921 10.1046/j.1365-2435.1999.00369.x, 1999.
922 [Rodriguez-Zaccaro, F. D., Valdovinos-Ayala, J., Percolla, M. I., Venturas, M. D., Pratt, R. B.,](#)
923 [and Jacobsen, A. L.: Wood structure and function change with maturity: Age of the vascular](#)
924 [cambium is associated with xylem changes in current-year growth. *Plant, Cell & Environment*,](#)
925 [42, 1816-1831, <https://doi.org/10.1111/pce.13528>, 2019.](#)
926 ~~44.~~ Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira,
927 A. A. R., Pullen, A. M., Doughty, C. E., Metcalfe, D. B., Vasconcelos, S. S., Ferreira, L. V.,
928 Malhi, Y., Grace, J., Mencuccini, M., and Meir, P.: Death from drought in tropical forests is
929 triggered by hydraulics not carbon starvation, *Nature*, 528, 119+, 10.1038/nature15539, 2015.
930 ~~45.~~ Sack, L., Cowan, P. D., Jaikummar, N., and Holbrook, N. M.: The 'hydrology' of leaves:
931 co-ordination of structure and function in temperate woody species, *Plant Cell Environ*, 26,
932 1343-1356, DOI 10.1046/j.0016-8025.2003.01058.x, 2003.
933 ~~46.~~ Savage, V. M., Bentley, L. P., Enquist, B. J., Sperry, J. S., Smith, D. D., Reich, P. B., and
934 von Allmen, E. I.: Hydraulic trade-offs and space filling enable better predictions of vascular
935 structure and function in plants, *P Natl Acad Sci USA*, 107, 22722-22727,
936 10.1073/pnas.1012194108, 2010.
937 [Schmidhalter, U.: The gradient between pre-dawn rhizoplane and bulk soil matric potentials, and](#)
938 [its relation to the pre-dawn root and leaf water potentials of four species. *Plant, Cell &*](#)
939 [*Environment*, 20, 953-960, <https://doi.org/10.1046/j.1365-3040.1997.d01-136.x>, 1997.](#)
940 [Seneviratne, S. I., Zhang, X., Adnan, M., Badi, W., Dereczynski, C., Luca, A. D., Ghosh, S.,](#)
941 [Iskandar, I., Kossin, J., Lewis, S., Otto, F., Pinto, I., Satoh, M., Vicente-Serrano, S. M., Wehner,](#)
942 [M., Zhou, B., and Allan, R.: Weather and climate extreme events in a changing climate, in:](#)
943 [Climate Change 2021: The Physical Science Basis: Working Group I contribution to the Sixth](#)
944 [Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Masson-](#)
945 [Delmotte, V. P., Zhai, A., Pirani, S. L., and Connors, C., Cambridge University Press,](#)
946 [Cambridge, UK, 1513-1766, 2021.](#)
947 [Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T.: A quantitative analysis of plant form-the pipe](#)
948 [model theory: I. Basic analyses, *Japanese Journal of ecology*, 14, 97-105, 1964.](#)
949 [Smith, D. D., Sperry, J. S., Enquist, B. J., Savage, V. M., McCulloh, K. A., and Bentley, L. P.:](#)
950 [Deviation from symmetrically self-similar branching in trees predicts altered hydraulics,](#)
951 [mechanics, light interception and metabolic scaling. *New Phytol*, 201, 217-229,](#)
952 [10.1111/nph.12487, 2014.](#)

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953 47. Sperry, J. S. and Love, D. M.: What plant hydraulics can tell us about responses to
954 climate-change droughts, *New Phytol*, 207, 14-27, 10.1111/nph.13354, 2015.

955 48. Su, R., Liu, H., Wang, C., Zhang, H., and Cui, J.: Leaf turgor loss point is one of the best
956 predictors of drought-induced tree mortality in tropical forest, *Front Ecol Evol*, 10, ARTN
957 974004: 10.3389/fevo.2022.974004, 2022.

958 Tyree, M. T. and Yang, S.: Water-storage capacity of Thuja, Tsuga and Acer stems measured by
959 dehydration isotherms: the contribution of capillary water and cavitation, *Planta*, 182, 420-426,
960 1990.

961 Wei, L., Xu, C. G., Jansen, S., Zhou, H., Christoffersen, B. O., Pockman, W. T., Middleton, R.
962 S., Marshall, J. D., and McDowell, N. G.: A heuristic classification of woody plants based on
963 contrasting shade and drought strategies, *Tree Physiol*, 39, 767-781, 10.1093/treephys/tpy146,
964 2019.

965 49. Wolfe, B. T.: Bark water vapour conductance is associated with drought performance in
966 tropical trees, *Biol Letters*, 16, ARTN 20200263: 10.1098/rsbl.2020.0263, 2020.

967 50. Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E.,
968 Condit, R., Dalling, J. W., Davies, S. J., Diaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell,
969 S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., and Zanne, A. E.: Functional traits and
970 the growth-mortality trade-off in tropical trees, *Ecology*, 91, 3664-3674, Doi 10.1890/09-2335.1,
971 2010.

972 51. Xu, C. G. and Gertner, G.: Understanding and comparisons of different sampling
973 approaches for the Fourier Amplitudes Sensitivity Test (FAST), *Comput Stat Data An*, 55, 184-
974 198, 10.1016/j.csda.2010.06.028, 2011a.

975 52. Xu, C. G. and Gertner, G. Z.: Reliability of global sensitivity indices, *J Stat Comput Sim*,
976 81, 1939-1969, 10.1080/00949655.2010.509317, 2011b.

977 53. Xu, C. G., McDowell, N. G., Fisher, R. A., Wei, L., Sevanto, S., Christoffersen, B. O.,
978 Weng, E. S., and Middleton, R. S.: Increasing impacts of extreme droughts on vegetation
979 productivity under climate change, *Nat Clim Change*, 9, 948-+, 10.1038/s41558-019-0630-6,
980 2019.

981 54. Xu, X. T., Medvigy, D., Powers, J. S., Becknell, J. M., and Guan, K. Y.: Diversity in
982 plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in
983 seasonally dry tropical forests, *New Phytol*, 212, 80-95, 10.1111/nph.14009, 2016.

984 55. Yang, S. D. and Tyree, M. T.: Hydraulic Resistance in Acer-Saccharum Shoots and Its
985 Influence on Leaf Water Potential and Transpiration, *Tree Physiol*, 12, 231-242, DOI
986 10.1093/treephys/12.3.231, 1993.

987

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