

# Implementing plant hydraulics in the Community Land Model

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## Key Points:

- A simplified soil-plant-atmosphere continuum model based on hydraulic theory is implemented in the Community Land Model (version 5).
- Prognostic leaf water potential replaces soil matric potential as the functional basis for water stress, thus reflecting how the leaf water supply (via the xylem network) and evaporative demand act in concert to determine plant water status and thus stomatal conductance and leaf gas exchange.
- Prognostic root water potential is used to implement hydraulic root water uptake, replacing the heuristic soil 'wilting' factor .

**Abstract**

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**1 Introduction**

Trees face emerging climate change risk globally [Allen *et al.*, 2010; Anderegg *et al.*, 2013a]. Understanding vegetation response is a high priority, both for discerning climate impacts and for modeling feedbacks to the carbon and hydrological cycles. In addition to stress from soil moisture drought, vegetation is susceptible to increasing atmospheric transpiration demand [Restaino *et al.*, 2016; Novick *et al.*, 2016a]. Increases in vapor pressure deficit (VPD) have occurred with warming [Ficklin and Novick, 2017; Seager *et al.*, 2015], and are associated with impacts on vegetation [Williams *et al.*, 2013; McDowell and Allen, 2015]. Significant uncertainty remains regarding how vegetation will respond to changes in hydroclimate within Earth System Models, feeding back onto the carbon cycle as vegetation mediates carbon uptake [De Kauwe *et al.*, 2017; Friedlingstein *et al.*, 2014].

Plant water stress parameterizations are important in Earth System Models, as they define vegetation regulation of surface fluxes (photosynthesis, transpiration) to water fluctuations. Vegetation water use strategies also modulate carbon uptake, creating a critical coupling between the Earth System's carbon and hydrological cycles [Green *et al.*, 2017]. Drought stress parameterizations (functions which relate simple metric of soil moisture status to leaf gas exchange) are widely used to define the response of stomatal conductance to vegetation water status that is used to attenuate transpiration, photosynthesis, and root water uptake with drying. The dynamics of water stress in models have broad effects on critical land surface processes [Joetzjer *et al.*, 2014]. On diurnal timescales, water stress parameterizations influence the partitioning of latent versus sensible heat with effects on surface temperature [Bonan *et al.*, 2014]. On longer timescales vegetation water use strategies regulate the global carbon and water cycles [De Kauwe *et al.*, 2015].

Many recent studies have aimed at advancing the representation of water flow through the Soil-Plant-Atmosphere continuum (SPAC) in land models [Xu *et al.*, 2016; Christoffersen *et al.*, 2016; Sperry *et al.*, 2017]. Explicit modeling of water flow through the SPAC adds complexity, but is consistent with evidence of dynamic regulation of vegetation water use in response to both soil and atmospheric drying [Sperry and Love, 2015]. Furthermore, via Darcy's Law, SPAC models have a robust physical basis. SPAC models involve new parameters, which presents new challenges [Drake *et al.*, 2017], but plant hydraulic trait information is available [Kattge *et al.*, 2011; Anderegg, 2015a], providing guidance on parameter estimation. and can be informative of forest vulnerability to drought [Choat *et al.*, 2012]. Likewise vegetation water status observations are available at a scale that is directly relevant to model development [Konings *et al.*, 2016; Grant *et al.*, 2016] and can be used to validate model results [Momen *et al.*, 2017; Konings *et al.*, 2017b].

The empirical representation of vegetation water stress in the Community Land Model (CLM) and other land surface models is a known deficiency, with implications for the representation of the dry/wet season in tropical rainforests [Powell *et al.*, 2013; Ukkola *et al.*, 2016].

In this study, we develop a plant hydraulic implementation within the recently released CLM version 5 (CLM5), based on hydraulic theory, which we refer to as the 'Plant Hydraulic Stress' (PHS) configuration. We analyse the dynamics of the new PHS model using site-level simulations that replicate the Caxiuanã, Brazil through-fall exclusion experiment [Fisher *et al.*, 2006].

Advancing the representation of the SPAC introduces the representation of vegetation water potential (discretized into leaf, stem and root elements) into the CLM, as well as an explicit representation of water supply, from the soil through the vegetation substrate. Tran-

spiration is attenuated with drought stress according to vegetation water status, capturing dynamic vegetation water use regulation. These changes have numerous implications, including

1. Leaf water potential serves as an improved metric for water status (compared to soil water or soil matric potential), since it reflects vegetation sensitivity to both soil and atmospheric drying, while serving as a diagnostic for excessive xylem tension and cavitation risk.
2. Modeling and plant hydrodynamics provides a framework for representing hydraulic redistribution [Lee *et al.*, 2005]
3. Modeling vegetation water potential allows improved connection to remote sensing observations (e.g. Vegetation Optical Depth) [Konings *et al.*, 2016].
4. Further, root water potential can be used to predict gradient-based root water uptake based on Darcy's law, replacing the previous empirical transpiration partitioning heuristic. This provides the means to vary, for example, the mean depth of extraction with changing soil water conditions.
5. The new model can represent a range of water use strategies, improving the connection between plant carbon allocation decisions and water availability.

#### SAY IN WHICH SECTION WE WILL FINE EACH PART

To assess the new model formulation, we carried out site-level simulations at Caxiuanã National Forest in Brazil, which features a critical biome (terra-firme moist tropical evergreen forest). Starting in 2001, a plot at this site was subjected to an approximately 50% percent precipitation through-fall exclusion. Due to the large drop in soil moisture at the precipitation exclusion site, we expect and observe [Fisher *et al.*, 2007] significant vegetation regulation of transpiration and photosynthesis.

In this paper we 1. Introduce the PHS theory and implementation in the CLM 2. Analyze the dynamics of modeled water stress, root water uptake and soil moisture profiles. 3. Compare PHS to the behaviour of the default CLM water stress configuration. 4. Discuss the benefits and limitations of the new model.

## 2 Model Description

### 2.1 Photosynthesis

The CLM5 photosynthesis model is described in Bonan *et al.* [2011], Thornton and Zimmermann [2007], and Oleson *et al.* [2013]. Photosynthesis is defined in three regimes: Rubisco-limited, light-limited, and export-limited following Farquhar *et al.* [1980] and Harley *et al.* [1992]. The implementation extends Sellers *et al.* [1996a,b] with co-limitation following Collatz *et al.* [1991].

CLM5 photosynthesis, in its default configuration, is a two-big-leaf model, with a sunlit and shaded leaf for each plant functional type [Thornton and Zimmermann, 2007; Dai *et al.*, 2004; Oleson *et al.*, 2013]. The canopy fluxes module iterates the solution for leaf temperature to satisfy the leaf surface energy balance, while environmental conditions are evolving. Within this, the photosynthesis module further iterates to solve for inter-cellular CO<sub>2</sub> concentration, balancing stomatal flux of CO<sub>2</sub> with photosynthetic assimilation flux of CO<sub>2</sub>.

### 2.2 Stomatal Conductance

CLM5 implements the Medlyn stomatal conductance model, which reconciles the empirical and optimal approaches to modeling stomatal conductance [Medlyn *et al.*, 2011]. Stomatal conductance of CO<sub>2</sub> is thus directly related to net photosynthesis ( $A_n$ ), CO<sub>2</sub> concentration at the leaf surface ( $C_a$ ), and the square root of the vapor pressure deficit near the

leaf surface ( $\sqrt{D}$ ).

$$g_s = g_0 + \left(1 + \frac{g_1}{\sqrt{D}}\right) \frac{A}{C_a} \quad (1)$$

The model features two parameters  $g_0$  ( $\mu\text{mol} / \text{m}^2 / \text{s}$ ) and  $g_1$  ( $\text{kPa}^{0.5}$ ). The  $g_0$  parameter is minimum stomatal conductance, representing cuticular and epidermal losses (small). The  $g_1$  parameter relates to the marginal water cost guiding the optimization of carbon assimilation. These parameters are plant functional type dependent.

The Medlyn model, derived from stomatal optimization theory, predicts stomatal conductance to maximize assimilation relative to water costs ( $A - \lambda E$ ), but does not resolve concurrent limitations to stomatal conductance associated with drought conditions. These water stress factors (in our case,  $f_w$ ), are used to represent stomatal and non-stomatal limitation not captured by the leaf-level stomatal conductance model (which can be thought of as a prediction of maximum stomatal conductance in these cases). To represent soil drought, and its impact on diffusive fluxes, land surface models typically include a ‘water stress factor’ ( $f_w$ , dimensionless, 0 to 1, formerly  $\beta_t$ ). Uncertainty remains within the literature for how to apply water stress factors to photosynthesis and/or stomatal conductance. [Zhou *et al.*, 2013; Novick *et al.*, 2016b; Sperry and Love, 2015].

In CLM,  $f_w$  multiplies the rate of maximum carboxylation ( $V_{\text{cmax}}$ ) as described in Oleson *et al.* [2013]. Other models opt for soil-moisture based stomatal limitation (linking the stomatal conductance model slope parameter to soil moisture), however, Lin *et al.* [2018] found that only  $g_0$  was sensitive to soil moisture (and not  $g_1$ ). Zhou *et al.* [2013] suggest that changes in assimilation tend to exceed those predicted by modulating  $g_1$  with soil moisture, but could be captured by changing  $V_{\text{cmax}}$ . Other field studies, however, suggest that  $V_{\text{cmax}}$  does not change with drought, whereby modeled  $V_{\text{cmax}}$  instead may implicitly account for mesophyll conductance changes [Flexas *et al.*, 2004].

In PHS, we opt for a simplified form of this stress approach, which seems to be consistent with field observations [Lin *et al.*, 2018]. Prognostic water stress ( $f_w$ , ranging from 0-1) attenuates stomatal conductance indirectly via multiplication of  $V_{\text{cmax}}$ . Water stress then lowers assimilation, which is coupled to stomatal conductance ([Medlyn *et al.*, 2011]).

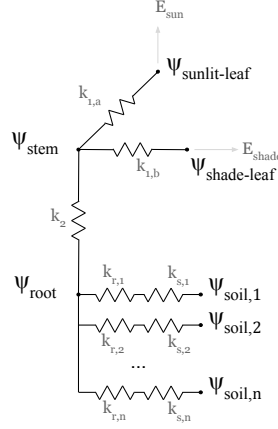
$f_w$  is modeled here as a function of leaf water potential ( $\psi_{\text{leaf}}$ ) (see Section 2.3.3), with stress increasing as  $\psi_{\text{leaf}}$  becomes more negative. This reflects the concept of hydraulic safety, with vegetation avoiding excessive xylem tension associated with risk of cavitation.

Utilizing leaf water potential adopts a framework where stomatal conductance optimized for carbon gain is concurrently limited by hydraulic constraints [Novick *et al.*, 2016b]. As a result, low soil water (bottom-up stress) can induce leaf moisture stress due to limited water supply while high atmospheric VPD can also induce leaf moisture stress by propagating a drying into the xylem (top-down stress).

Much recent work has focused on alternative constraints on plant hydrodynamics, especially in response to drying soils [Manzoni *et al.*, 2013a; Novick *et al.*, 2016b; Zhou *et al.*, 2014]. This includes how plants manage the risk of cavitation associated with increasing xylem tension [Sperry *et al.*, 1998]. [Sperry *et al.*, 2017], for example, argue that theory based on hydraulic costs (define) could be used instead of optimizing of  $A - \lambda E$ . Otherwise, the marginal water cost might be adjusted based on soil water status by adjusting  $\lambda$  or Medlyn  $g_1$  [Manzoni *et al.*, 2013a], but this may underestimate drought effects on photosynthesis \*expand on this-RF\*[Zhou *et al.*, 2013; Lin *et al.*, 2018]. A hybrid approach, combines stomatal optimization with hydraulic constraints and/or so-called non-stomatal limitation, where stress attenuates  $V_{\text{cmax}}$  or mesophyll conductance (both of which feed back through photosynthesis to lower stomatal conductance) [Egea *et al.*, 2011; Novick *et al.*, 2016b]. [\*link this back to which options are used in PHS -RF\*]

## 2.3 Plant Hydraulic Stress (PHS)

The PHS model within CLM5 uses hydraulic (Darcy's) law and a corresponding electrical circuit analogy (Figure 1), to model the flow of water through the SPAC. The hydraulic framework is used to diagnose water stress associated with increasing xylem tension and to calculate the root water uptake in each of (in this case) 20 vertically discretized soil layers.



**Figure 1.** Plant hydraulic circuit analog schematic

### 2.3.1 Hydraulic schematic and segmentation

PHS solves for the set of SPAC vegetation water potential values ( $\psi_{\text{root}}$ ,  $\psi_{\text{stem}}$ ,  $\psi_{\text{shade-leaf}}$ ,  $\psi_{\text{sun-leaf}}$ ) that matches water supply (root water uptake) to water demand (transpiration), while maintaining continuity of water flow throughout the SPAC. Segmentation and other model design decisions followed a preference for a simplified implementation that whenever possible conformed to existing CLM model structure.

At each node in the circuit diagram in Figure 1 we model water potential, and, between nodes, we resolve the flux of water. The choice of nodes for segmentation is designed to take advantage of field-measured hydraulic traits and to allow for differences in segment parameterizations [Simonin *et al.*, 2015; Sperry and Love, 2015]. As in other versions of the CLM, PHS uses vertically discretized soil layers and a two-layer (sunlit vs. shaded) canopy. Water uptake from the different soil layers is assumed to operate in parallel; a typical assumption justified by higher resistance in lateral versus central roots (e.g. Williams *et al.* 2001). We further separate resistance through the soil matrix from the resistance through the root tissue [Williams *et al.*, 1996]. Specifics on the parameterization of conductance for each segment are provided in Appendix B.1.

### 2.3.2 Water supply

Water supply is modeled via Darcy's Law, where flow of water ( $q$ ) is the product of the path hydraulic conductance ( $k$ ) and the gradient in water potential (accounting for changes in gravitational potential). Equation 2 represents the flow from a generic node 1 to node 2.

$$q = -k (\psi_2 - \psi_1 - \rho g \Delta z) \quad (2)$$

PHS does not represent plant tissue water storage (or capacitance, using the electrical circuit analogy). Capacitance significantly complicates the water potential solution [Celia *et al.*, 1990] and is challenging to parameterize [Bartlett *et al.*, 2016]. However, buffering

of water stress provided by tissue water storage could potentially be important especially on sub-daily timescales [Meinzer *et al.*, 2009; Epila *et al.*, 2017], whereby its inclusion may be warranted in future model generations.

Vegetation segment conductance is modeled following empirical xylem vulnerability curves [Tyree and Sperry, 1989], where segments lose conductance with increasing xylem tension related to cavitation and embolism [Holbrook *et al.*, 2001]. The vulnerability curves model loss of conductance relative to maximum conductance using two parameters:  $c_k$ , a sigmoidal shape-fitting parameter, and  $p_{50}$ , the water potential at 50% loss of segment conductance (following Gentine *et al.* [2016]).

Both  $c_k$  and  $p_{50}$  can be estimated from field experiments [Sack *et al.*, 2002], and  $p_{50}$  is available in the TRY trait database [Kattge *et al.*, 2011]. Parameterization based on  $p_{50}$  aligns with the call for a transition to models that use a wider range of plant functional trait data in their parameterization [Anderegg, 2015a]. The loss of xylem conductivity is based on lower terminal water potential ( $\psi_1$ ) as is typical in other simplified models [Xu *et al.*, 2016], but may underestimate the integrated loss of conductivity [Sperry and Love, 2015].

$$k = k_{\max} 2^{-\left(\frac{\psi_1}{p_{50}}\right)^{c_k}} \quad (3)$$

PHS models root, stem, and leaf tissue conductances according to equation 3. The parameterization of  $k_{\max}$  varies by hydraulic segment (see details in Appendix B1). The conductance across the soil matrix to the root surface follows Williams *et al.* [2001] and Bonan *et al.* [2014] and estimates a characteristic distance between the bulk soil and the root surface, to facilitate length-scaling of soil conductivity. Bulk soil resistivity is based on Clapp and Hornberger [1978] as described in Oleson *et al.* [2013]. Further details are provided in Appendix B1.

### 2.3.3 Water demand

Vegetation water demand and stomatal regulation is based on the Medlyn stomatal conductance model (see Section 2.2), which we adjust using the water stress factor  $f_w$ . As discussed earlier,  $f_w$  is based on leaf water potential [Klein and Niu, 2014], and multiplies  $V_{\max}$ , thus attenuating photosynthesis, and thus also stomatal conductance and transpiration.

As leaf water potential declines (because of transpiration) and xylem tension increases, transpiration is attenuated relative to its maximal value. The maximum transpiration ( $E_{\text{sun},\max}$ ,  $E_{\text{shade},\max}$ ) is defined as the value that results from Medlyn stomatal conductance in the absence of water stress (achieved by setting  $f_w = 1$ ). The fraction of maximum transpiration is modeled with a two-parameter sigmoidal function (Equation 4).

$$\begin{aligned} E_{\text{sun}} &= E_{\text{sun},\max} 2^{-\left(\frac{\psi_{\text{sun-leaf}}}{\psi_{50}}\right)^{c_k}} \\ E_{\text{shade}} &= E_{\text{shade},\max} 2^{-\left(\frac{\psi_{\text{shade-leaf}}}{\psi_{50}}\right)^{c_k}} \end{aligned} \quad (4)$$

Where  $\psi_{50}$  is the leaf water potential at 50% loss of transpiration and  $c_k$  is a sigmoidal shape-fitting parameter.

We define  $f_w$  as the ratio of attenuated to maximal stomatal conductance (Equation 5). Maximum stomatal conductance ( $g_{s,\text{sun},\max}$ ,  $g_{s,\text{shade},\max}$ ) is computed as the stomatal conductance in the absence of water stress, i.e.  $f_w = 1$ . The attenuated stomatal conductance ( $g_{s,\text{sun}}$ ,  $g_{s,\text{shade}}$ ) is then the stomatal conductance associated with the PHS module water flow solution, which matches vegetation water supply with vegetation water demand (Section 2.3.4).

$$f_{w,sun} = \frac{g_{s,sun}}{g_{s,sun,max}}$$

$$f_{w,shade} = \frac{g_{s,shade}}{g_{s,shade,max}} \quad (5)$$

Whereas the water supply parameters (see Section 2.3.2) relate to hydraulic traits often measured in the field, the hydraulic demand parameters  $\psi_{50}$  and  $c_k$  reflect the emergent property of hydraulic limitations to transpiration and must be empirically derived (WHAT ABOUT PLC CURVES?).

CLM also features two empirical stomatal control parameters, which are the soil matric potentials where stomata are either fully closed ( $\theta_{wilt}$ ) or fully open ( $\theta_{crit}$ ) (see Section 3). Recent modeling studies have proposed different forms of relationship between stomatal regulation with water stress [Sperry *et al.*, 2017; Xu *et al.*, 2016; Christoffersen *et al.*, 2016] and thus this representation remains the topic of active research .

### 2.3.4 PHS solution

PHS solves for the set of vegetation water potential values ( $\psi$ ) that matches water supply (root water uptake) to water demand (transpiration), while satisfying continuity across the four water flow segments (soil-to-root, root-to-stem, stem-to-leaf, and leaves-to-transpiration). At each time step, PHS computes the flux divergence  $f$  (representing the mismatch of flow in and out of each segment for a given set of vegetation water potential values  $\psi_i$ , and iteratively updates  $\psi$  until convergence is reached in terms of divergence,  $f \rightarrow 0$ .

$$\psi = \begin{bmatrix} \psi_{sun} \\ \psi_{shade} \\ \psi_{stem} \\ \psi_{root} \end{bmatrix} \quad (6)$$

$$f(\psi) = \begin{bmatrix} E_{sun} - q_{sun} \\ E_{shade} - q_{shade} \\ q_{sun} + q_{shade} - q_{stem} \\ q_{stem} - \sum_{j=1}^n q_{root,j} \end{bmatrix} \quad (7)$$

$$A = \frac{df}{d\psi} \quad (8)$$

While  $|f| > 0$

$$\Delta\psi = A^{-1} f(\psi_i)$$

$$\psi_{i+1} = \psi_i + \Delta\psi \quad (9)$$

The numerics are tractable because  $f$  has analytical derivatives and  $A$  (a 4x4 matrix with six null entries) is easy to invert when well-conditioned. Supply and demand converge, because transpiration demand decreases with more negative leaf water potentials and supply increases with more negative leaf water potentials. Within a set of PHS iterations (9), transpiration is assumed to be linear with  $f_w$ .

The PHS loop is nested within iterations for intercellular CO<sub>2</sub> concentration and leaf temperature. The non-linear relationship between  $f_w$  and transpiration is resolved through iteration for converging  $f_w$  alongside intercellular CO<sub>2</sub>. Details on the numerical implementation are provided in Appendix Section B.1.



### 3 Water stress factor, SMS vs. PHS

PHS alters the transpiration beta function ( $\beta_t$ , colloquially BTRAN, Equation 10), SAY WAHT IT IS which is the phenomenological soil water stress function in used in prior versions of CLM, as described in *Oleson et al.* [2013]. Because the name  $\beta_t$  is associated with this specific plant hydrodynamics representation, we opt to rename the variable to the water stress factor  $f_w$ . Throughout this paper we refer to the original CLM plant hydrodynamics framework as SMS (soil moisture stress), as compared to the newer implementation described here, PHS (plant hydraulic stress). We adopt this terminology (in lieu of CLM4.5 vs. CLM5), because SMS is still deployable with CLM5. In this section we present the SMS version of  $f_w$  and outline the differences as compared to PHS

With PHS, we interpret  $f_w$  as a drought safety mechanism, attenuating stomatal conductance to avoid excessive xylem tension associated with very negative leaf water potential. As such,  $f_w$  is parameterized as a function of prognostic leaf water potential. With SMS,  $f_w$  is calculated based on soil matric potential, as a root-fraction weighted average potential departure from an empirical soil layer wilting factor (Equation 10). Recent studies suggest that the SMS parameterization introduces model bias in turbulent fluxes [*Bonan et al.*, 2014] and contributes to unrealistic drought response of photosynthesis and stomatal conductance [*Powell et al.*, 2013].

In SMS, the variable  $f_w$  is unitless, ranging from 0 to 1, with 1 corresponding to no water stress, and 0 corresponding to fully water stressed. It is calculated based on a root-fraction weighted average of soil layer wilting factor ( $w_i$ ), which is a bounded linear function of soil water potential ( $\psi_i$ ) relative to PFT parameters defining the soil potential with stomates fully open ( $\psi_o$ ) and fully closed ( $\psi_c$ ), among the soil layers  $i = 1, \dots, n$ . Note that root fraction ( $r_i$ ) sums to 1, by definition.

$$f_w = \sum_{i=1}^n r_i w_i \quad (10)$$

$$w_i = 0 \leq \frac{\psi_i - \psi_c}{\psi_o - \psi_c} \leq 1 \quad (11)$$

#### 3.1 Root water uptake in SMS vs. PHS

Such parameterizations (WHICH ONES?) have primarily been examined with application to stomatal conductance, but they are also used to define vegetation soil water extraction. Each timestep, the transpiration flux solution must be distributed among the vertically discretized soil layers. In the SMS framework, the transpiration sink is partitioned by layer according to the soil layer wilting factor and root fraction.

In both stress parameterizations,  $f_w$  multiplies  $V_{cmax}$  to attenuate photosynthesis and stomatal conductance with soil water stress. With SMS, it is also directly used for modeling vegetation water extraction from the soil column. The total transpiration ( $T$ ) is partitioned among the soil layers based on the  $f_w$  wilting factor. Within each soil layer, the contribution to total transpiration ( $q_i$ ) depends on the layer root fraction and wilting factor, normalized by  $f_w$ :

$$q_i = \frac{r_i w_i}{f_w} T \quad (12)$$

Contrary to the heuristic SMS parameterization, the PHS implementation adopts a physically-based hydraulic framework, where the root water uptake ( $q_i$ ) is the product of the hydraulic conductance ( $k_i$ ) and the gradient in water potential ( $-\Delta\psi$ ) driving the flow, i.e. obeying Darcy's law. That gradient is the difference between the root water potential ( $\psi_{root}$ )



and the layer soil water potential ( $\psi_i$ ), minus changes in gravitational potential, following Darcy's law.

$$q_i = -k_i \Delta\psi$$

$$\Delta\psi = (\psi_{\text{root}} - \psi_i - \rho g \Delta z)$$
(13)

For comparison between SMS and PHS, we recast (12) into the hydraulic framework: defining  $T_{\text{max}}$ , such that:  $T = f_w T_{\text{max}}$  to replace  $T$  in (12), and replacing  $w_i$  in (12) with the formula from (11).

$$q_i = \frac{T_{\text{max}}}{\psi_o - \psi_c} r_i (\psi_i - \psi_c)$$
(14)

This yields SMS analogs for the hydraulic conductance and gradient terms of Equation 13.

$$k_i = r_i \frac{T_{\text{max}}}{\psi_o - \psi_c}$$

$$\Delta\psi = \psi_c - \psi_i$$

constrained by:

$$\Delta\psi = \begin{cases} 0 & \text{if } \psi_i < \psi_c \\ \psi_c - \psi_o & \text{if } \psi_i > \psi_o \end{cases}$$
(15)

We use this formulation to discuss some of the implications for root water uptake from the former SMS parameterization of water stress (Equation 15).

### 3.2 Constant pulling potential

With SMS, that gradient is defined for each soil layer as the difference between the soil water potential in that layer ( $\psi_i$ ) and a constant parameter, the soil water potential when stomata are fully closed ( $\psi_c$ ). This parameter serves as the vegetation “pulling” potential for calculating the soil transpiration sink.

Using a constant wilting point is inconsistent with extensive evidence from the field of dynamic vegetation water potential, and cohesion tension theory (CITATIONS NEEDED) driving the transpiration flow. Likewise the values for  $\psi_c$  are quite negative, (-2.5 MPa for broadleaf evergreen tropical, BET, forests). *Fisher et al.* [2006] measured midday stem potential consistently higher than -0.5 MPa during the wet season, and on average -1.69 and -1.53 MPa during the dry season in the control and exclusion plots, respectively.

### 3.3 Conductance dynamics

In SMS, in lieu of dynamic vegetation water potential, intra-day SMS soil sink dynamics derive from a highly variable conductance (CLARIFY). As inferred in Equation 15, SMS conductance is modeled as a function of  $T_{\text{max}}$ , and three constant parameters.  $T_{\text{max}}$  is highly dynamic, responding to the diurnal course in transpiration demand. This is inconsistent with general principles of porous media flow, where conductivity is a function of the hydraulic architecture and its wetted status. Likewise, this representation of conductance does not represent the characteristic phenomenon where vessels lose conductance with drying.

### 3.4 No dependence on belowground carbon allocation

As is typical in water stress parameterizations, the SMS conductance is scaled by layer using an area basis, here using the relative vertical root fraction is used. With PHS, an absolute measure of root biomass is used (see Appendix Equation B.7), so that the belowground water cycle interacts with carbon allocation to the roots. An absolute measure better conforms with the physics of porous media flow and better responds to varying carbon allocation

strategies. For example, with SMS, if root mass doubles in every soil layer, the root access to water remains unchanged.

### 3.5 Lacks penalties for extraction from depth

Both PHS and SMS account for the effect of decreasing root area with depth (PHS, root area; SMS, root fraction), but PHS implements two other penalties for extracting water from deep in the soil column that are missing from SMS. The first is minor, but water extracted from depth must overcome gravity, amounting to about 0.01 MPa per meter in depth. This is missing from SMS and included with PHS. Likewise, SMS ignores the fact that hydraulic conductance is generally taken to scale with the inverse of conducting length. Deeper roots feature longer root tissue conducting length, and root spacing within the soil is less dense, requiring longer conducting distances across the soil matrix. In PHS, both these processes result in diminished hydraulic conductance (UNCLEAR).

### 3.6 Constraints

With SMS, the gradient in water potential is constrained between 0 and the range of soil potential between parameters for stomata fully open and closed (Equation 15). The upper constraint caps the gradient in water potential when soil potential reaches the value for stomata fully open ( $\psi_o = -0.65$  MPa for BET). Darcy's Law predicts that the gradient in water potential would continue to increase until saturation matric potential. The lower constraint caps the gradient in water potential at zero, disallowing negative gradients. However, reversed water fluxes, caused by positive gradients in water potential from root to soil, have been observed in the field [Burgess *et al.*, 1998]. Both constraints are eschewed with PHS.

## 4 Experiment Description

All four simulations in this paper use the same development version of CLM5 (development version r270, [https://github.com/ESCOMP/ctsm/releases/tag/clm4\\_5\\_18\\_r270](https://github.com/ESCOMP/ctsm/releases/tag/clm4_5_18_r270)).

The four simulations are used to assess the impact of the plant hydrodynamics model (PHS vs. SMS) on a through-fall experiment (i.e., with either ambient or 60% through-fall excluded), with all other model components and forcing shared. Simulations are run offline (uncoupled from an active atmospheric model), spanning from 2001 through 2003, utilizing the satellite phenology (SP) mode of CLM5 in which vegetation state (LAI, canopy height) is prescribed and biogeochemistry is inactive. All simulations start from the same initial conditions, which are obtained from a 9-year spin-up that repeats the PHS/Ambient simulation three times. To avoid duplication, descriptions of site characteristics, forcing data, and observational sap flux, can be found in Fisher *et al.* [2007].

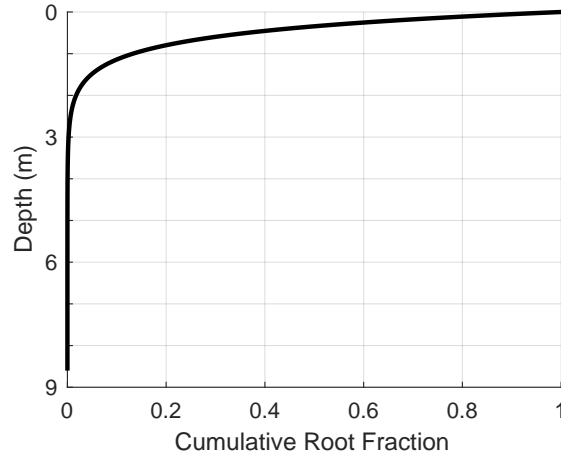
### 4.1 Parameter Values and Through-fall Exclusion

Selected parameter values concerning vegetation hydrodynamics are presented in Table 1. All other parameters use the default values associated with the r270 version of CLM5. Informed by Fisher *et al.* [2008], we tuned soil hydraulic parameters and through-fall exclusion rates to reasonably capture the observed soil water dynamics (Fisher *et al.* [2007] Figure 4), Supplementary Figure ??). Likewise, we tuned  $k_{max}$  and  $g_1$  parameters to improve the fit to sap flux observations in the ambient simulation. The object of this paper is to present the dynamical impact of PHS to clearly describe model functionality. Model skill and parameter sensitivity will be assessed in follow-up studies.

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**Table 1.** Select parameter values

CLM name	Full Name	Symbol	Value
kmax(1)	Maximum Sun Branch Conductance	$k_{1a,max}$	$4e-8 \text{ s}^{-1}$
kmax(2)	Maximum Shade Branch Conductance	$k_{1b,max}$	$4e-8 \text{ s}^{-1}$
kmax(3)	Maximum Stem Conductivity	$k_{2,max}$	$4e-8 \text{ m/s}$
krmax	Maximum Root Conductivity	$k_{r,max}$	$6e-9 \text{ m/s}$
psi50	Water potential at 50% loss of conductivity	$\psi_{50}$	-1.75 MPa
ck	Vulnerability shape parameter	$c_k$	2.95
smpso	Soil potential with stomata fully open	$\psi_o$	-0.65 MPa
smpsc	Soil potential with stomata fully closed	$\psi_c$	-2.5 MPa
medlyn_intercept	Medlyn intercept	$g_0$	$100 \mu\text{mol} / \text{m}^2 / \text{s}$
medlyn_slope	Medlyn slope	$g_1$	$6 \text{ kPa}^{0.5}$
n	Soil porosity to 4.64 meters	$n$	0.42
n	Soil porosity beyond 4.64 meters	$n$	0.28
hksat	Saturated soil hydraulic conductivity	$k_{s,max}$	$3e-5 \text{ m/s}$
sucsat	Saturated soil matric potential	$\psi_{sat}$	461 Pa
bsw	Brooks-Corey parameter	$b$	6



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**Figure 2.** Cumulative rooting distribution

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## 5 Results

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### 5.1 Vegetation water potential

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PHS introduces prognostic vegetation water potential to CLM at four locations within the plant structure: at the root, stem, shaded leaf, and sunlit leaf. Under ambient conditions, 2003 dry season (September-October-November) model average sunlit leaf water potential is -1.65 MPa at midday (local time 12-14h, Figure 3a). The midday pressure drop is primarily between  $\psi_{root}$  and  $\psi_{stem}$ , representing the root collar and upper stem, respectively. Under TFE, model midday leaf water potential decreases to -2.31 MPa (Figure 3b). Partitioned among the segments of the SPAC, the change in leaf water potential (totaling -0.66MPa) due to TFE is: -0.44MPa soil potential, -0.66MPa soil-to-root, +0.45MPa root-to-stem, and -0.001MPa stem-to-leaf. This comports with previous evidence that seasonal changes in hydraulic resistance are larger belowground [Fisher *et al.*, 2006].

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Describing Figure 3c seasonal cycle, LWP values in range of fisher2006 if on the low side, but stem too low in ambient and TFE effect was not observed in the field.

**Table 2.** Root-zone soil potential <sup>a</sup> (MPa) terciles for Figure 5

Simulation	T1	T2
SMS, Ambient	-0.01	-0.54
SMS, TFE	-0.29	-1.74
PHS, Ambient	-0.01	-0.05
PHS, TFE	-0.05	-0.33

<sup>a</sup>SMS values correspond to daily mean root-fraction weighted soil potential. PHS values correspond to predawn root water potential.

## 5.2 Stress factor

Average midday stress values from the two models are comparable during the 2003 dry season (Figure 4). Under ambient conditions, the average stress factor values are 0.59 and 0.54 for SMS and PHS, respectively (dry season, midday), decreasing to 0.16 and 0.21, with TFE. While the SMS stress factor has minimal diurnal variability (Figure 4a), PHS features increased stress at midday (Figure 4b), tracking the drop in leaf water potential (Figure 3b,c). Likewise, the PHS stress factor responds to both soil moisture and VPD (Figure 5c,d), while SMS responds only to soil moisture (Figure 5a,b). This results in more wet season (FMA) stress with PHS (as compared to SMS) under both ambient and TFE conditions (Figure 6a-d).

## 5.3 GPP and Transpiration

The two models predict similar total GPP across 2002-2003 under TFE, 3.96 kg/m<sup>2</sup> (SMS) and 4.00 kg/m<sup>2</sup> (PHS), but GPP is lower for PHS under ambient conditions (4.86 kg/m<sup>2</sup>) as compared to SMS (5.46 kg/m<sup>2</sup>, Figure 6e-h). The standard deviation of daily total GPP (2002-2003) is smaller for PHS (0.49, 1.55 g/m<sup>2</sup>/d for AMB/TFE) than for SMS (1.53, 2.73 g/m<sup>2</sup>/d). Transpiration seasonality is comparable between the two models (Figure 7a,b), but with a larger amplitude for SMS. PHS yields a better fit to field observations of daily sap flux (see Section zqz), with higher R<sup>2</sup> and lower RMSE compared to SMS under both ambient and TFE conditions (Figure 7c-f).

## 5.4 Hydraulic conductance

In Figures 8 and ??, we compare conductance values derived from the PHS and SMS implementations. With SMS,  $k$  is not explicitly modeled, so instead we infer  $k$ , by dividing root water uptake  $q_i$ , by  $\Delta\psi$  as defined in Equation 15. We interpret the constraint that  $\Delta\psi$  be greater than or equal to zero to mean that conductance is zero in non-conforming cases, which we extend to  $k = 0$  when  $\Delta\psi < 1$  kPa. For our analyses, we consider only points when transpiration is greater than 4 W/m<sup>2</sup>, which improves the tractability of inferring conductance, given that SMS root water uptake is precluded absent transpiration (REPHRASE).

For Figure 8a,b, conductance is plotted from Soil Layer 3 (spans from 6 to 12 cm below ground), for all points during 2003 when transpiration is greater than 4 W/m<sup>2</sup> (n=7752). For Figure ??a,b, conductance is averaged daily, subject to the same restrictions. Average intra-day standard deviation is reported for FMA, by which we calculate a daily standard deviation of complying points, and report the average over the 89 days.

## 5.5 Root water uptake

Vertical profiles of the rate of root water uptake are presented in Figures 9a and 10a, averaged over SON and FMA, respectively. This is plotted as average cumulative rate of root water uptake, starting at depth (8.6 meters). Time series of total root water uptake are also provided (Figs 9b,c, 10b,c). We plot total cumulative water extracted from near the surface over time in Figures 9b and 10b, accompanied by that extracted from depths beyond 20 centimeters in Figures 9c and 10d. We chose 20 centimeters as the break point based on the vertical profiles of root water uptake, and with a preference for not splitting any of the discrete soil layers. Soil Layers 1-4 span 0 to 0.2 meters, and Soil Layers 5-20 span 0.2 to 8.6 meters. Time series of total cumulative ambient precipitation are shown for comparison (Figs 9b and 10b).

## 5.6 Hydraulic redistribution

Hydraulic redistribution refers to flows of water between soil layers through vegetation substrate. To calculate total HR, we sum the negative root water uptake fluxes ((i.e., root to soil fluxes) across all soil layers. Total HR, partitioned by month and by daytime versus nighttime is shown in Figure 11. Note that over the course of a day or season, HR can occur without net negative root water uptake. For example, hydraulic lift may occur at night, moving water from deep in the soil column up to near the surface, which is then more readily available for transpiration during the following day. This can result in HR occurring even when there is net positive root water uptake. This type of feature is evident in Figure 9, where there is net positive root water uptake throughout the soil column over the 2003 dry season, even when there is significant HR into the near-surface layers (Fig 11).

## 5.7 Soil moisture

The vertical profile soil water potential under 60% TFE is plotted in Figure 12 (SMA, DO NOT SAY THIS IS PLOTTED BUT DESCRIBE RESULTS AND MENTION FIGURE). The range in soil potential is much larger within the SMS paradigm, which made it difficult to plot both panels with the same color scale. In order to preserve information in the PHS plot, we opt for a scale of 0 to -1 MPa, as compared to 0 to -3 MPa for SMS. When comparing column average soil potential, we use separate definitions, which reflect each paradigm's representation of soil water availability. With SMS, we opt for a root-fraction weighted average, following from Equation 14. This is a poor measure for PHS, because it neglects gravitational contributions and the appropriate root area basis. Instead we opt for predawn (defined at 5AM) root water potential, which, given minimal transpiration at night, is in equilibrium with the soil column.

# 6 Discussion

## 6.1 The promise of plant hydraulics

Plant hydraulics have promised to improve model predictions of vegetation response to climate change [Sperry and Love, 2015], especially if parameter ranges and model complexity can be constrained [Alistair et al., 2017]. Numerous site-level models have deployed plant hydraulics (e.g. Williams et al. [1996]; Sperry et al. [1998]; Bohrer et al. [2005]), and studies show vegetation water potential can improve predictions of stomatal response to the environment [Sperry et al., 2017; Anderegg et al., 2017]. More recently hydraulics have been coupled to global models [Bonan et al., 2014; Xu et al., 2016; Christoffersen et al., 2016], but most Earth System Models do not incorporate plant xylem.

In this study, we implement plant hydraulic theory within CLM5, using vegetation water potential to modulate leaf gas exchange and root water uptake. We model water potential according to circuit analogy (Figure 1), which captures expected diurnal and seasonal dy-

namics of leaf water potential (Figure 3). Under ambient conditions hydraulic resistance is largest from root-to-stem (Figure 3a), while the added resistance from TFE is primarily from soil-to-root (Figure 3b), consistent with previous results [Fisher *et al.*, 2006].

Concerns exist in the literature regarding hydraulic model complexity and parameterization [Verhoef and Egea, 2014; Drake *et al.*, 2017], which informed our model design (see Section 2.2). Support for hydraulic models better mortality and productivity [McDowell *et al.*, 2018; Choat *et al.*, 2012], complexity can be managed, by [Bartlett *et al.*, 2016; Powell *et al.*, 2018]. LWP can be monitored in the field [Boyer, 1967] and has been shown to correlate with remote sensing products [Momen *et al.*, 2017], which could provide crucial validation. Parameter values can be measured in the field [Sack *et al.*, 2002] and are available in the TRY database [Kattge *et al.*, 2011].

## 6.2 Water stress and stomatal conductance

Stress, which was previously based on soil potential, switches to leaf potential, imparting a diurnal cycle (Figure 4). As such, stress now depends on transpiration demand, and, in turn, VPD and solar radiation (Figures 5.A.1). Medlyn does already reduce stomatal conductance based on VPD, but based on  $A-\lambda E$ . Here we are trying to impart xylem tension stress, allowing plants to avoid cavitation and embolism. Support for this in the literature [Novick *et al.*, 2016b; Sperry *et al.*, 2017], but still no consensus on the best functional form [Zhou *et al.*, 2013].

The water stress factor follows a seasonal cycle, with lower (indicating more stress) values during the dry season, but with a smaller amplitude compared to the control model (Figure 6a-d). As a result PHS features less seasonal variability in GPP, especially under ambient conditions (Figure 6e-h). The xylem tension constraint in PHS imparts a negative feedback on GPP. Factors increasing GPP (e.g. more light) also increase xylem tension and stress, which limits GPP. Restrepo-Coupe *et al.* [2017] show that GPP increases at Caxiutla during the dry season, suggesting that PHS improves the GPP seasonal cycle.

However, PHS underestimates the seasonal cycle in transpiration under ambient predictions, with less variability than sap flux observations (Figure 7a,c). Likewise, we produce a high bias in transpiration under TFE, similar to previous evidence showing that models tend to underestimate the effect of TFE [Powell *et al.*, 2013]. Considerable uncertainty remains regarding the appropriate functional form of water stress. Further work could examine other permutations of water stress, and/or concurrent improvement in photosynthesis parameters and model structure. While a work in progress, PHS does improve transpiration predictions, with lower RMSE and higher correlation compared to the control model, albeit with model tuning (Figure 7).

## 7 Results and Discussion

### 7.1 Modeling vegetation water potential

The models are compared for the 2003 dry season (Sept-Oct-Nov or SON) at Caxiutla for two experiments: the first with ambient rainfall (AMB), and the second with 60% of rainfall excluded, or 'through-fall exclusion' (TFE), Figure 3.

In the ambient simulation (Fig 3a), average midday water potentials are -1.96, -1.95, -1.94 MPa for sunlit leaf, shaded leaf, and stem, respectively. With through-fall exclusion (TFE), as expected the midday water potentials decrease to -2.77, -2.76, -2.75 MPa, respectively (Fig 3b).

Both panels show the characteristic drop in water potential around midday and the expected sequencing with the leaf water potentials more negative than the stem potential, which is more negative than the root potential. The sequencing is difficult to distinguish from the



plot, where the stem, sunlit, and shaded leaf water potential curves nearly overlap for both experiments because there is only very small drop in potential between the stem and leaves.

The small difference between leaf and stem water potentials results from minimal resistance to water flow across these segments. (LINK THIS TO THE PREVIOUS STATEMENT) The current PHS parameterization of stem-to-leaf resistance is relatively simple compared to the literature [Franks *et al.*, 2007] and could be advanced in future versions.

TFE lowers average midday sunlit leaf water potential by 0.81 MPa compared to the ambient simulation, during SON-2003 (dry season). This change in leaf water potential can be partitioned into the change in soil water potential, the change in potential drop from soil-to-root, and the change in potential drop from root-to-leaf.

Beginning with the change in soil water potential, in the ambient simulation, average predawn (5AM) root water potential (an integrated measure of soil water potential) is -0.075 MPa. With TFE, it falls to -0.36 MPa, resulting in a decrease in predawn root water potential of 0.28 MPa relative to the ambient simulation. The difference between midday and predawn root water potential (which stands in for potential drop from soil-to-root) is lowered by 1.06 MPa in the simulate TFE plot (from -0.06 MPa, ambient, to -1.12 MPa, TFE).

The difference between sunlit leaf and stem water potential at midday acts in the opposite direction, changing from -1.83 MPa in the ambient simulation to -1.29 MPa with TFE, attenuating the drop in leaf water potential by 0.54 MPa.

Predicted water potential values are comparable with field observations, where average dry season leaf water potential was measured as -2.47 MPa [Fisher *et al.*, 2006]. With PHS, modeled change in leaf water potential due to TFE is -0.81 MPa, which can be partitioned into -0.28 MPa predawn root water potential, -1.06 soil-to-root drop, +0.53 root-to-leaf drop. The drop in water potential across the stem partially abates the change in the soil and roots due to TFE.

Though stem conductance decreases with drying, transpiration also decreases, yielding a net effect of a smaller drop in water potential across the stem. This is consistent with findings in Fisher *et al.* [2006] that most of the whole-plant resistance is above ground, but that added resistance from drying is predominately sourced? below ground. Likewise Fisher *et al.* [2006] found evidence of isohydric behavior, where plants manage water loss through stomata to regulate leaf water potential, which is consistent with results here of reduction in potential drop across the stem. However, PHS shows declines in midday leaf water potential due to TFE, but Fisher *et al.* [2006] found no significant observed difference between ambient and TFE dry season leaf water potential. This could indicate that our parameters do not result in sufficiently isohydric behavior.

Many facets of our hydraulic representation are simplified relative to the literature, reflecting that in a model designed to operate at the global scale, there is a tradeoff between added complexity and parameter reduction. The current PHS parameterization omits vegetation capacitance, which may be important for accurately modeling the diurnal cycle of water stress especially in tropical rainforests [Meinzer *et al.*, 2009]. Further, hydraulic conductance hysteresis and permanent cavitation are absent from the PHS vulnerability parameterization, whereby xylem segments fully regain conducting capacity upon re-wetting. This limits the influence of drought legacy, which has been shown to be significant for forest mortality [Anderegg *et al.*, 2013b].

Similar to other simplified models [Xu *et al.*, 2016], loss of conductance is based on lower terminus water potential, which may underestimate integrated loss of conductivity [Sperry and Love, 2015]. These simplifications each serve to lessen the parameter and/or computational burden of PHS. Our objective was to simplify the plant hydraulic representation for this initial implementation, acknowledging that more comprehensive process representation may prove necessary for future model versions.



## 7.2 Stress factor, annual dynamics

Figure ?? shows monthly mean values of the water stress factor, gross primary productivity, and transpiration over the three-year simulations for PHS versus SMS under ambient and 60% through-fall exclusion conditions. Under ambient through-fall conditions, the SMS simulation features less stress (Fig ??b), with no stress ( $f_w > 0.99$ ) in 24 out of 36 months.

PHS predicts more stress (Fig ??a), with stress in sync with the evolution of mid-day leaf water potential (Figure 3). As a result,  $f_w$  is generally lowest in September (Fig ??e). ZQZ need to go back and output btran proper. Alternatively, SMS predicts no stress ( $f_w > 0.99$ ) during any of the three Septembers of the ambient simulation. Instead  $f_w$  is generally lowest in December.

SMS has the most stress in December, which is associated with lower soil moisture (Supp Fig ??). While soil moisture is lowest in December, transpiration demand is higher in September, which is the month with the most stress in the PHS simulations (Fig ??a). To achieve high transpiration rates, vegetation must operate with a large gradient in water potential from soil-to-leaf, associated with increased xylem tension and risk of cavitation. As such, leaf water potential declines with soil moisture drying, but also with increasing transpiration demand (Fig 3). PHS is designed to represent hydraulic limitation to transpiration associated with xylem tension, which responds to both soil drying and increased transpiration demand (i.e. higher VPD) [Sperry and Love, 2015]. The latter is absent from the SMS formulation.

Through-fall exclusion (which initiates on November 1, 2001) adds stress in both the SMS and PHS simulations (Fig ??c,d). The added stress is greater and the onset faster with SMS. In both cases, the effect of TFE accumulates in time, with less photosynthesis and transpiration in 2003 compared to 2002. This is not reflected in the sap flux observations, which feature a more rapid onset of reduced transpiration, and similar transpiration between 2002 and 2003.

In both SMS and PHS, soil water is used to buffer shortfalls in precipitation versus transpiration (Supp Fig A.8). (UNLCEAR). Transpiration in PHS is less sensitive to TFE, which can be partly attributable to differences in root water uptake (see Section 7.5). PHS utilizes more deep soil water to mitigate declines in root-zone soil moisture as water flow is imposed to go down water potential gradients. In the dry season surface drying also decreases soil-root conductance so that it is easier to extract moisture from deeper layers, consistent with observations based on isotopes (CITATION).

Another dynamic feature of PHS is that hydraulic limitation establishes a negative feedback loop between photosynthesis/transpiration and water stress. If photosynthesis increases, generally stomatal conductance and transpiration increase. This causes more negative leaf water potential and an associated increase in water stress, which attenuates photosynthesis. This diminishes variability in transpiration and photosynthesis, relative to SMS (Fig ??c-f). The strength of this feedback is subject to parameters controlling maximum conductance and the stomatal response to leaf water potential. Quantifying variability in diffusive fluxes with PHS as compared to SMS and observations is an important topic for future studies (See Lawrence et al in prep).

Significant uncertainty exists in soil and root hydraulic parameters as well as the root distribution, whereby better behavior may exist within the plausible parameter space. Likewise, the parameter values for both stress implementations could be tuned further. Observations indicate the trees here adopt an isohydric behavior, where declines in soil moisture are tightly coupled with reduced transpiration, which mitigates decreases in leaf water potential [Fisher et al., 2006]. The parameter values employed for these simulations may be insufficiently isohydric (GIVE REFERENCE AND DEFINE ISOHYDRICITY), which could explain limited sensitivity to TFE relative to observations.

### 7.3 Stress factor, diurnal dynamics

In addition to changes in the annual cycle, PHS introduces a diurnal cycle to  $f_w$  (Fig ??a). The SMS version of  $f_w$  exhibits almost no diurnal variability (Fig ??b) since water stress is therein a function of soil water potential, which lacks a significant diurnal cycle. PHS uses a function of leaf water potential (e.g. Fig 3a,b) to model water stress, which responds to diurnal variation in transpiration demand (via changes in VPD, solar radiation, etc.).

The relationship of water stress with VPD and soil potential is shown in Figure ?. To emphasize the relationship with VPD, data are subsetting for a small window in downwelling solar radiation (between 400 and 425 W/m<sup>2</sup>). For the TFE simulations (panels *c* and *d*), we also subset for years 2002 and 2003, because TFE was not active during most of 2001. Points are colored based on soil potential, partitioning the data from each plot into terciles, blue points are wettest, red points driest, and yellow points intermediate. For details on the soil water classification and radiation subsetting see Section zqz (THIS SHOULD BE IN CAPTION NOT MAIN TEXT).

The SMS version of  $f_w$  has a clear dependence on soil potential, but no relationship with VPD (Fig ??b,d), as expected. Drier soil potentials are associated with lower values of  $f_w$  (which corresponds to more stress). With PHS, higher VPD results in more stress (Fig ??a,c). Under ambient through-fall conditions (Fig ??a), soil water potential has minimal influence. With TFE, stress responds to both VPD and soil water (Figure ??c). Similar effects are shown in response to downwelling solar radiation (Supp Fig A.1).

Water stress is applied to capture limitations with declining water status that are not reflected within the Medlyn stomatal optimization theory (which only optimizes  $\delta E/\delta A$ , and thus does not take water supply into account). CLM implements non-stomatal limitation by multiplying  $V_{cmax}$  by  $f_w$ . Though there is limited evidence of down-regulation of  $V_{cmax}$  [Flexas *et al.*, 2006], this was the best option within CLM for applying stress through the GPP term of the stomatal conductance model, in accordance with field observations [Lin *et al.*, 2018; Zhou *et al.*, 2013]. If in future versions of CLM, mesophyll conductance is represented, it may be a more appropriate avenue for achieving the same effect. (MERGE WITH PREVIOUS DISCUSSION, TRY AVOIDING REPETITIONS A MUCH AS POSSIBLE)

Total soil water content (or departure from saturation) is a typical basis for diagnosing water status and stress [Drake *et al.*, 2017], which is in line with an SMS-type approach. While capturing supply limitations, this framework neglects effects of transpiration demand on xylem tension. Given constant stomatal conductance, xylem tension increases with declining soil water, but also with increasing vapor pressure deficit. While VPD sensitivity is included in the Medlyn model, it serves to mitigate increasing water costs, without consideration of cavitation. Evidence suggests that vegetation employ water use strategies to mitigate the risk of cavitation associated with increasing xylem tension [Sperry *et al.*, 1998; Fisher *et al.*, 2006; Choat *et al.*, 2012]. Utilizing leaf water potential as the basis for water status reflects this constraint. This may be especially important given projected increases in VPD associated with warming.

### 7.4 Hydraulic conductance: PHS vs SMS (implied)

Soil-to-root conductance ( $k_{sr}$ ) is explicitly represented in PHS, modeled as a function of soil potential (zqz). With SMS,  $k_{sr}$  is not explicitly modeled, but it can be inferred, by dividing root water uptake by the gradient in water potential (see Section zqz). Comparing conductance under these two paradigms serves to highlight differences in how water supply is modeled. In , we plot the time-series of conductance values from Soil Layer 3 (spanning from 6 to 12 centimeters below the surface) under ambient through-fall conditions during 2003, along with precipitation over the same period (PLUG IN CAPTION).

During the wet season, PHS conductance is greater than SMS by more than two orders of magnitude (Fig 8a,b). PHS conductance is generally steady through the wet season (Fig 8a), followed by a slow decline over the dry season with short resurgence episodes associated with rain events. The SMS implied conductance features more variability relative to the mean (Fig 8b). During FMA-2003, average intra-day standard deviation of Layer 3 conductance is  $4.6\text{e-}12\text{ s}^{-1}$  with PHS and  $9.9\text{e-}12\text{ s}^{-1}$  with SMS. In an absolute sense the SMS standard deviation is about twice as large as PHS. The difference is larger in a relative sense, as this corresponds to 0.08% of the mean FMA conductance with PHS and 62.9% of the mean FMA conductance with SMS.

The SMS inferred conductance is tethered to transpiration (see Section 3), which leads to the high variance and a clear diurnal cycle (Supp Fig A.2). Instead PHS calculates  $k_{sr}$  based on soil hydraulic properties and root xylem vulnerability, which better reflects the physics (flow has to be down water potential gradients) and the temporal dynamics of transpiration demand.

As a result conductance is less variable, with the expected responses to drydown (loss of conductance) and re-wetting (increased conductance). This is further demonstrated in Figure 7, where we plot the daily mean conductance from Soil Layer 3. With 60% through-fall exclusion (Fig7a, dotted line), PHS conductance decreases, whereas with SMS, the daily mean conductance increases (Fig7b). The latter SMS increase is unrealistic and conflicts with extensive literature demonstrating loss of conductivity with drying (CITATIONS).

Despite two orders of magnitude difference in conductances, total root water uptake during FMA2003 is not very different (23.4 cm PHS vs. 24.9 cm SMS). The reason for these smaller differences, is that the extraction gradient compensate for the differences in conductance. The SMS extraction gradient is measured relative to  $\psi_c$  (a parameter defining soil potential with stomates fully closed), which equals -2.5MPa for BET. The PHS extraction gradient is relative to root water potential which during 2003 (ambient through-fall) varies between -0.02 and -0.23 MPa. Fisher *et al.* [2006] measured stem water potential consistently higher (less negative) than -0.5MPa.

With TFE, PHS Layer 3 conductance can approach the values seen in SMS. The average Layer 3 conductance with PHS for August 2003 (60%TFE) is  $4.75\text{e-}11\text{ s}^{-1}$  as compared to  $3.89\text{e-}11\text{ s}^{-1}$  for SMS. This is a result of the orders of magnitude response of PHS soil-to-root conductance to changes in soil potential (Supp Fig A.3) (UNCLEAR MODIFY SENTENCE). This conforms with typical soil hydraulics, where large changes in conductance occur with drying. On the other hand, SMS conductance has no clear relationship with soil potential (Supp Fig A.3).

## 7.5 Root Water Uptake: PHS vs SMS

Root water uptake is the flux of water ( $q_i$ , mm/s) extracted from each of the vertically discretized soil layers ( $i = [1, 2, \dots, n]$ ). These fluxes are used as the soil transpiration sink terms within the Richards' equation [Oleson *et al.*, 2013] and, summed over the soil column, are equivalent to the transpiration flux. As described above (and in Section 3), PHS adopts a hydraulic framework for root water uptake.

PHS simulations (black color), feature more surface extraction than with SMS, especially under ambient through-fall conditions (Fig9a), during the 2003 dry season. The time-series of PHS total cumulative extraction (cm) from near-surface soil (Fig9b) responds to precipitation (Fig9d), with increased surface extraction after rain events.

Under ambient conditions the SMS partitioning of extraction between near-surface and depth is not sensitive to precipitation. In PHS near-surface extraction decreases by 40% with TFE (8.12 vs 13.51 cm), while, SMS features a 24% increase in absolute terms (5.28 vs 6.55 cm, Fig 9b). Under TFE, both PHS and SMS extract minimal water from between

0.5 and 4m, (3.18 cm and 0.56 cm, respectively, over the three months). Both compensate by increasing extraction from below 4m, but PHS to a much larger extent, which corresponds to overall significantly more root water uptake during TFE.

Root water uptake dynamics respond to changes in hydraulic conductance and/or changes in the gradient in water potential. PHS has more access to water at depth under TFE, associated with higher conductance values. With decreasing soil potential, hydraulic conductance decreases with PHS, but can increase with SMS (7.4). Instead SMS is limited by the extraction gradient, with root water uptake declining to zero as soil potential approaches -2.5 MPa (Supp Fig A.4). PHS is more sensitive to changes in soil water potential, with stronger decreases in root water uptake in response to drying within a soil layer (Supp Fig A.4). In response, PHS features increases in near-surface water uptake after rain and decreases with TFE.

The wet season (Feb-Mar-Apr FMA-2003), features more and steadier rain (Fig 10d). PHS responds with an increase in the proportion of water extraction from near the surface relative to SON. Under ambient conditions net extraction is zero beyond about 38 centimeters depth (Fig 10a, solid black line). In comparison, SMS extracts more than half its water from beyond 1 meter in depth even during the wet season (Fig 10a, solid gray line). With TFE, PHS extraction is negative beyond 20 centimeters, indicating hydraulic redistribution (Fig 10c). Over the three month FMA-2003 period, there is no net root water uptake below 20 centimeters depth, but rather a deposition of about 10 cm of water is simulated.

In both the wet and dry season, PHS features significantly more root water uptake from the near-surface layers (0 to 20cm in depth). Modeled surface extraction is especially high over the wet season under through-fall exclusion conditions, summing to 32.7 cm over 89 days. By comparison SMS extracts 4.8 cm under the same conditions. With a soil porosity of 0.42, the top 20 cm of soil hold only 8.2cm of water at saturation.

Conductances are higher with PHS (see Section 7.4), which allows for higher rates of root water uptake, especially from moist soil layers. Likewise PHS better reflects penalties for extraction from depth (Section 3, favoring near-surface water all else being equal. The highest rates of root water uptake (relative to layer size) occur from Soil Layer 2, after rain events during the dry season (Supp Fig A.7). Lowering maximum conductance can attenuate high rates of extraction, if observations conflict with model output.

The PHS configuration allows for more realistic root water uptake, incorporating hydraulic theory. SMS does not accurately represent xylem loss of conductance or the dynamics of vegetation water potential. Both are difficult to parameterize, given the scarcity of data describing states, traits, and fluxes underground. PHS offers a process connection between soil potential and leaf water potential, which may be used to evaluate the model.

## 7.6 Hydraulic redistribution

During the wet season surface extraction supplies transpiration, but is also redistributed into lower soil layers. Hydraulic redistribution has been observed in the field [*Oliveira et al.*, 2005], and is not represented in the SMS version of the CLM [*Lee et al.*, 2005]. which sets root water uptake to zero if the gradient in water potential is negative.

For HR to occur into a soil layer, the soil potential must be more negative (drier) than the  $\psi_{\text{root}}$  (see Figure . During the day, transpiration requires a gradient in water potential from soil-to-root, which lowers  $\psi_{\text{root}}$ , decreasing the amount of HR. Therefore, in PHS, more HR occurs at night, in accordance with observations and theory [*Oliveira et al.*, 2005; *Lee et al.*, 2005].

HR is predominately downwards during the wet season (FMA), serving to diminish the gradient between the newly-wetted surface and still-dry depths (Supp Figs A.6,A.7). Redistribution occurs in both directions during the dry season (SON), downwards after rain events,

and upwards with drying. Only with TFE, and only during the dry season, is there significant extraction beyond 6 meters (Figs 8, 9). There is very little water deposited at depths beyond 6 meters at any point in either simulation.

Under ambient conditions simulated HR in PHS totals to 41.3 cm (10.3 cm during the day, 31.0 cm at night), Figure 11. HR declines slightly to 37.0 cm (11.5 cm day and 25.5 cm night) with TFE. For reference, total transpiration over the same time period was 120 and 99 cm for ambient and TFE conditions, respectively. The TFE simulation has less HR overall, but more HR during wet months, Feb-June.

Increased downwards? HR within the TFE plot occurs in Feb-June, associated with the drier TFE soils and larger gradients in soil potential from surface to depth. HR is lower in January, and July-December with TFE. Similar to during the wet months the gradient in soil potential (in this case from depth to surface) is larger with TFE. However, the soils overall are so dry with TFE during the dry months, that loss of conductance from soil-to-root counteracts the large gradient, resulting in lower HR.

The dynamics of HR with PHS align with observations, with more HR at night, and HR occurring in both directions vertically [Burgess *et al.*, 1998]. The absolute values of HR are difficult to assess, given limited observations.

In PHS, Allowing HR to occur into the top layer of the soil column significantly degraded modeled soil evaporation (not shown). We opted to omit the first top Layer (spanning 0 to 2 cm below ground) soil-to-root hydraulic conductance, to prevent HR from over-supplying water for soil evaporation.

### 7.6.1 Is hydraulic redistribution a feature or a liability?

HR is a natural consequence of using Darcy's Law to model root water uptake - when hydraulic gradients are reversed, HR should occur. As such it is naturally included within a plant hydraulics model with multiple soil layers and is an emergent behavior of respecting hydraulic flow down gradient of potentials. In ESMs, where soil moisture is typically resolved vertically, interfacing the plant hydraulics with a multi-layer soil naturally accounts for HR. Other models, similar to the SMS paradigm, disallow HR by constraining root water uptake to be positive [Xu *et al.*, 2016].

Most literature models force the model with a single bulk soil water potential  $\psi_s$ , which precludes HR [Fisher *et al.*, 2007; Bonan *et al.*, 2014; Sperry *et al.*, 2017]. Christoffersen *et al.* [2016] expand beyond a single  $\psi_s$  horizontally, representing soil elements at different characteristic distances from the root surface, but still feature a single soil layer in the vertical dimension.

Likewise HR is likely sensitive to the representation of vegetation tissue capacitance and below-ground hydraulic segmentation (CITATIONS NEEDED).

Hydraulic redistribution has the impact of reducing the variance in the availability of water for plant transpiration, potentially at odds with observations of interannual variation (see Lawrence *et al.* in prep. Tang *et al.* 2015) Observations of HR are extremely difficult, in unequivocal detection of HR involves the observation of reverse flow along transport roots, typically at rates close to the detection threshold of sap flow monitoring systems. Therefore, the degree to which HR actually occurs is unclear. While there is some first-order benefit to plants of moving water from deep soil to surface layers to allow more transpiration, this water is then also available for competition with other shallow-rooted plants, and for evaporative processes. Further, cavitation of fine roots in shallow soils might explicitly act as a 'fuse' to prevent loss of water from the plant into dry soil layers (Kotowska *et al.* 2015) - a process not explicitly resolved here. Therefore we view this first implementation of HR into the default versions of the CLM as a 'null' hypothesis for the functioning of this process, and as a platform to allow further refinement from the plant hydraulics community.



## 7.7 Soil moisture profile

The column total soil water in all four simulations is initialized at 2.66 meters (over an 8.6-meter soil column) (SAY WHY). The change in total soil water is small under ambient conditions, decreasing by 0.3cm with PHS and 9.6cm with SMS over the three-year simulations. Root zone soil potential is lower with SMS, with a root-fraction-weighted average soil potential of -0.42 MPa during November 2003. The equivalent metric from PHS, average predawn root water potential, is -0.08 MPa.

Under 60% through-fall exclusion, the change in soil water is -1.12 meters with PHS and -0.94 meters with SMS, relative to the ambient simulations (Supp Fig A.8).

With SMS, root-fraction-weighted average soil potential is -2.18MPa during November 2003, whereas PHS average predawn root water potential is -0.37MPa (Figure 12). Observations of root-zone potential based on gravity-corrected predawn leaf water potential are -0.17 +/- 0.10 MPa under ambient conditions, and -0.71 +/- 0.31 MPa with through-fall exclusion (also in November 2003) [Fisher *et al.*, 2007]. The SMS root-weighted water potential is 1.81 MPa drier (from a soil water potential perspective) because the SMS continues to extract water from dry layers with high fractions of roots, further drying these layers and decreasing the root-weighted water potential (see Section 7.4). Further, PHS has more access to deep soil water under dry conditions (Fig 9), which mitigates declines in soil potential near the surface.

While PHS better matches observations of root-zone soil potential, we hesitate to make conclusions about model skill due to parameter uncertainty and due to the fact that these values may be sensitive to tuning (see Section 4.1), as well as the fact that both models feature high biases in transpiration relative to observations.

Darcy's Law establishes that water flow is proportional to the gradient in total water potential. With PHS, this gradient is measured relative to dynamic  $\psi_{\text{root}}$ . With SMS, this gradient is measured relative to a constant parameter,  $\psi_c$ , the soil water potential at which stomates fully close. This approach is required without prognostic vegetation water potential, but yields unsatisfactory dynamics that do not comply with the physics of porous media flow (see Section 7.4). Furthermore, it seems that  $\psi_c$  has historically been tuned for its effects on diffusive fluxes, without specific attention to the effect on soil moisture dynamics (Can someone else back me up on this? Is there a way to cite this?).

This is problematic because soil moisture dynamics are very sensitive to  $\psi_c$ . Root water uptake halts when soil potential reaches  $\psi_c$  (Section 3), setting an effective minimum soil potential, a situation that is apparent in Figure 12 where soil water potential for SMS stays at approximately -2.5 MPa, which is the value of  $\psi_c$  for evergreen tropical broadleaf trees (?). This feature is clearer in Figure A.10, where soil layers can be seen to dry out quickly, but not beyond -2.5 MPa (with the exception of Soil Layers 1 and 2, which are influenced by bare soil evaporation). The effect of  $\psi_c$  extends to ambient through-fall conditions (Fig A.9), but over a smaller spatial and temporal domain. PHS has more flexibility, due to dynamic root water potential, so there is not the same tendency to dry out quickly to a specific level. Instead minimum soil water potential for PHS gets lower each dry season throughout the TFE simulation (Fig 12a).

[Add some material looking at the vertical profile of soil moisture in the models vs observations?]

Soil water dynamics in CLM are sensitive to the representation of root water uptake, but due to the scarcity of observational constraints, vertically-resolved soil moisture predictions are challenging to evaluate.

With PHS, because we're modeling vegetation water potential, we can utilize a hydraulic framework, which offers a well-established physical basis and a clear improvement

in model structure. SMS root water uptake has problematic model structure, seemingly no empirical basis, and intuitively does not look good on soil water dynamics. PHS improves model structure, but it also adds parameters that are difficult to constrain.

PHS offers leaf and stem water potential observations, which are downstream of soil potential, and could be an exciting opportunity to interface with observations. While PHS seems a clear improvement over SMS, which does not comport well with fundamental aspects of hydraulic theory, further work on the representation of root water uptake in models is needed to validate both soil water states and fluxes.

## 8 Conclusion

### 8.1 Caveats

Modeling stomatal conductance and photosynthesis, especially subject to water stress, is an area of ongoing research. We use the Medlyn model coupled to a hydraulic stress function that attenuates  $V_{cmax}$ . This complies with observations [Lin *et al.*, 2018; Zhou *et al.*, 2013] that stress applied through  $g_1$  underestimates attenuation of photosynthesis. However, there is no direct evidence of declines in  $V_{cmax}$  with drought [Flexas *et al.*, 2006], whereby future work may seek to represent mesophyll conductance in CLM.

The model hydraulic supply representation is simplified, to reduce the model parameter and computational burdens. No capacitance. No integration of xylem or soil conductances vulnerability, instead based on lower node. No hysteresis in loss of conductance, xylem instantly regain conductance upon re-wetting. Leaf conductance simplified. Soil layers fully parallel, soil potential constant each time step.

Parameter uncertainty is significant. Notions of hydraulic architecture will never perfectly fit on this modeling scale, especially in a PFT paradigm. Field measurements of hydraulic traits will help constrain parameter ranges, but mostly only aboveground. Flux observations can help to tune stress parameters. Parameter estimation for root functioning is significantly more challenging, given the difficulty in underground trait observations. Likewise observational constraints of vertically-resolved states and fluxes underground are scarce. Follow-up work will be geared towards parameter estimation and assessing model skill.

### 8.2 Utility of modeling vegetation water potential

The PHS configuration of the CLM5 is, to our knowledge, the first Earth System Model with a representation of plant water potential running in its default configuration. In this paper, we have described the model implementation, and illustrated a comparison of the model dynamics for a tropical rainforest site subjected to water limitation, given that prediction of rainforest responses to drought is one of the key uncertainties in the ESM predictions. Overall, the new model behaviour differs from the default configuration in ways that are expected, given its structural properties, and in many cases, provides better correspondance with the observations that the default structure.

In this paper, however, we do not undertake a comprehensive assessment of which model structure performs better, given the substantial parametric uncertainty in both models, and the dependence on numerous other features of the CLM external to water stress representation that contribute to model-observation divergences - in this case in particular, the overestimation of unstressed transpiration by both versions of the model compared to the observations.

In lieu of this type of assessment, we propose that the new PHS model structure 1) is more closely aligned with known plant hydraulics theory, 2) provides significantly improved connections to real-world observational data streams (of leaf and stem water status, sap flow, percent loss conductance) and 3) represents known features of ecohydrological function that



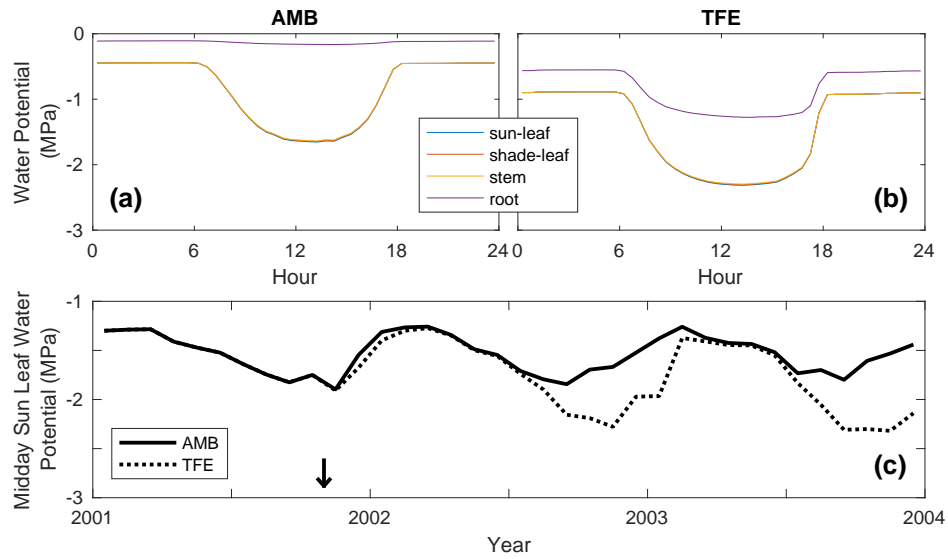
914 the default model cannot capture, including hydraulic redistribution, changes in the depth of  
915 water uptake with drought stress, plant embolism impacts on gas exchange and responses of  
916 water uptake to changes in leaf:root ratios.

917 This will be the final conclusions. Any comments on overall takeaways?

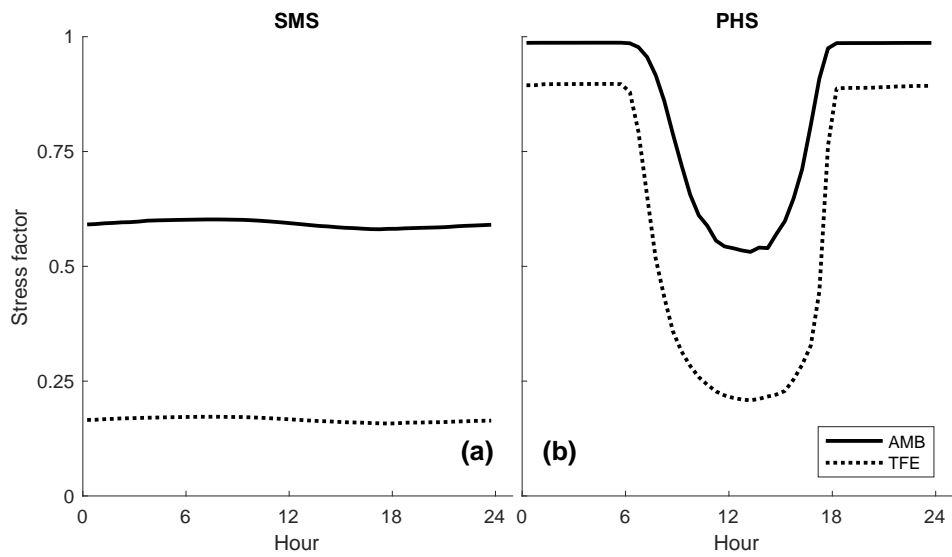
918 PHS models vegetation water potential. This offers structural improvements for stress  
919 and for root water uptake. Stress now functions with hydraulic limitation.

## 920 **9 Acknowledgments**

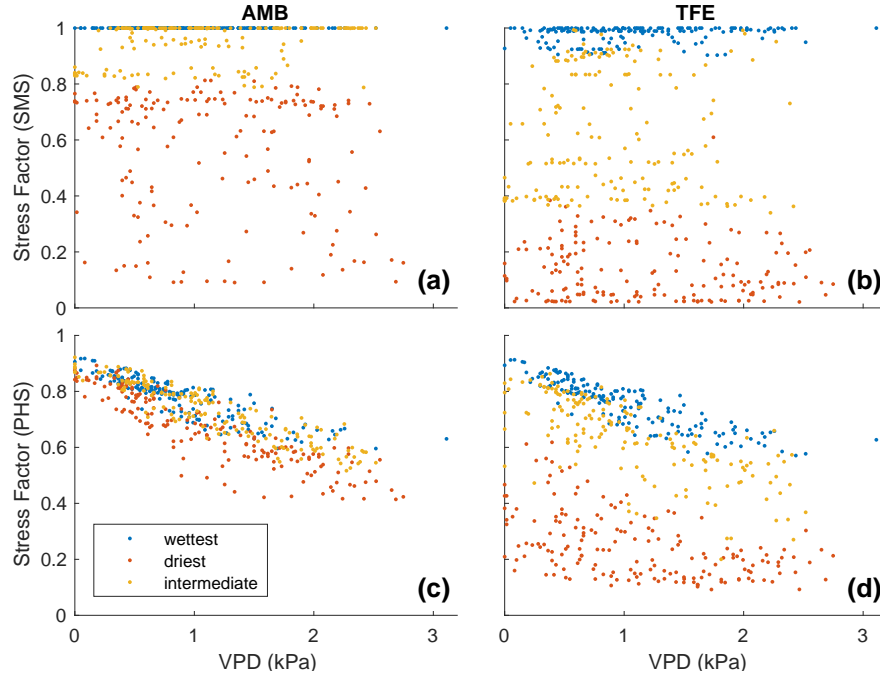
## 10 Figures



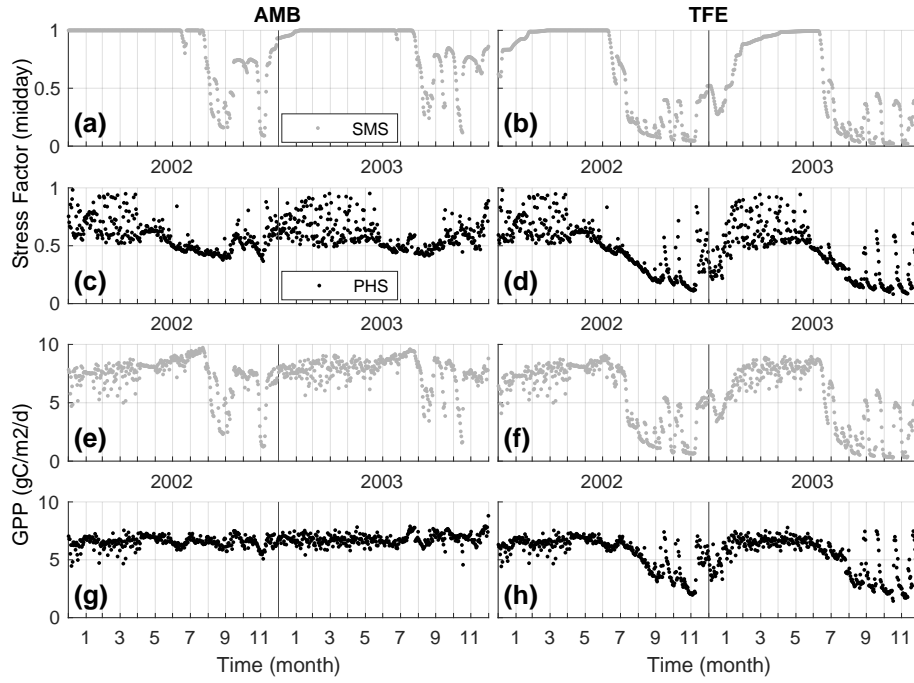
**Figure 3.** Modeled vegetation water potential at Caxiuanã, Brazil. (a) 2003 dry season (SON) diurnal mean, ambient through-fall conditions, (b) 2003 dry season diurnal mean, with 60% TFE. Curves are drawn for sunlit leaf, shaded leaf, stem, and root water potentials, with the first three mostly overlapping. (c) Monthly average midday (12h-14h) leaf water potential, under ambient (solid line) and TFE (dotted line) conditions. Note that TFE begins Nov 1, 2001, as indicated by the vertical arrow.



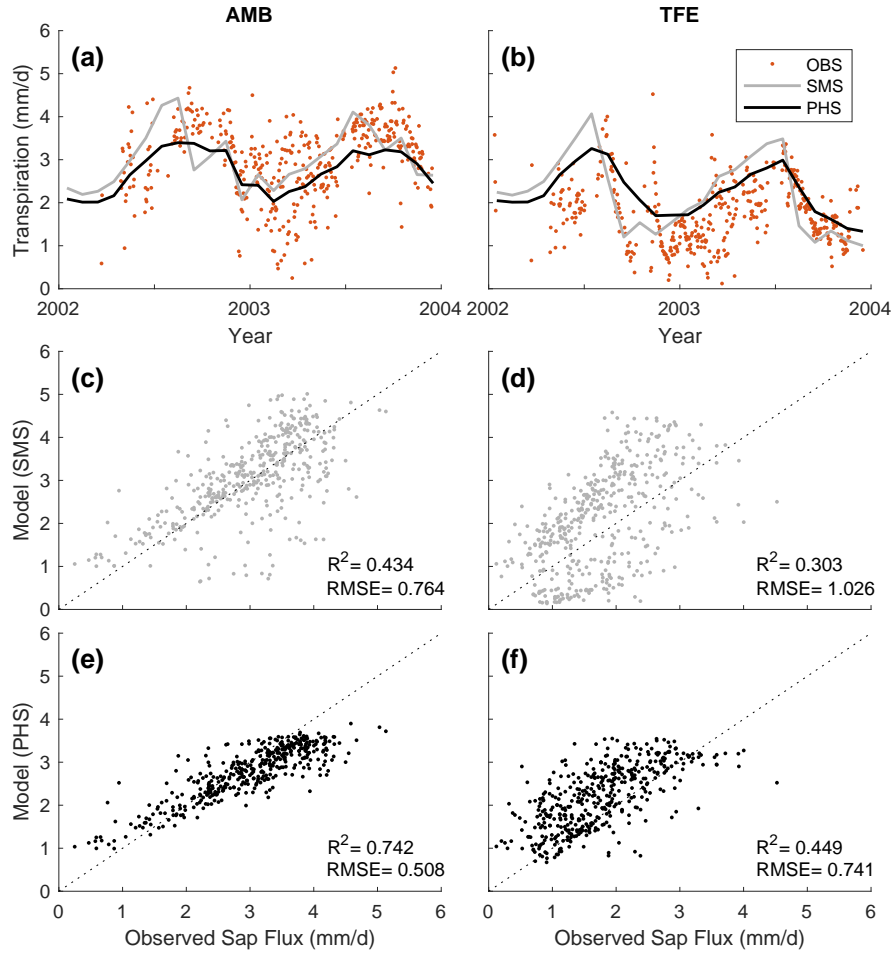
**Figure 4.** 2003 dry season (SON) diurnal mean water stress function for (a) SMS, and (b) PHS. Note that the water stress factor equals 1 when there is no stress and 0 when fully stressed.



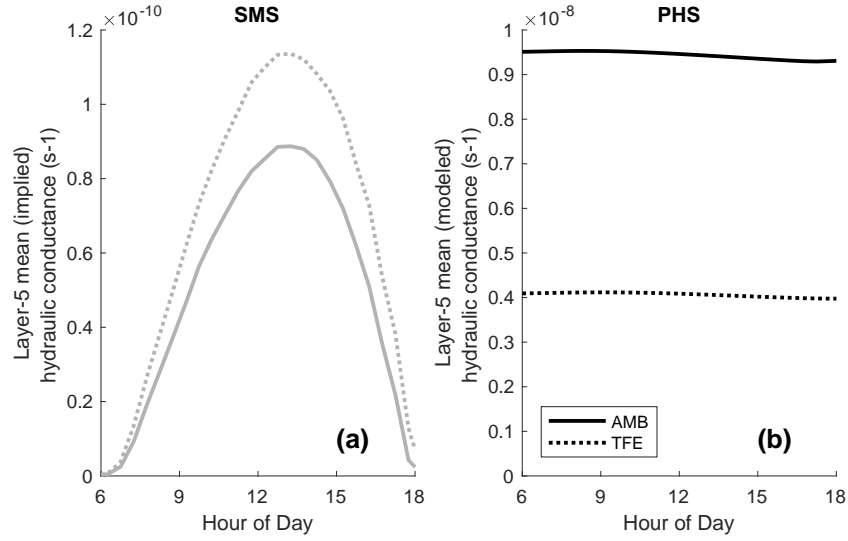
**Figure 5.** Water stress factor versus vapor pressure deficit (2002-2003), for timesteps with downwelling shortwave radiation between 400 and 425 W/m<sup>2</sup> (n=515). Radiation is controlled to highlight the relationship with VPD, the reverse (controlling for VPD) is shown in Figure A.1. For SMS (a,b), data are subdivided based on average soil matric potential, weighted by root fraction. For PHS (c,d), data are subdivided based on predawn (5h) root water potential. Blue dots represent the wettest tercile, yellow dots represent the intermediate tercile, and red dots represent the driest tercile (see Table 2).



**Figure 6.** Daily stress factor (midday, averaged over 12h-14h) and GPP during 2002-2003 under ambient (left) and TFE (right) conditions. Output from the SMS configuration (a,b,e,f) are plotted with gray color, while output from the PHS configuration (c,d,g,h) are plotted in black.

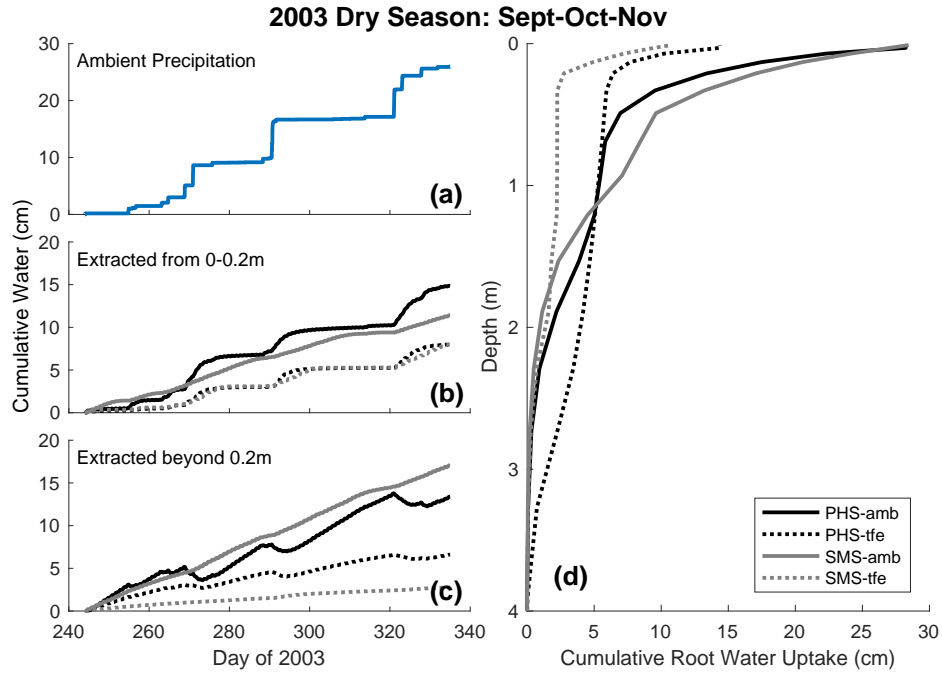


**Figure 7.** (a,b) Monthly mean water stress function. The water stress factor equals 1 when there is no stress and 0 when fully stressed. (c,d) Monthly mean transpiration ( $\text{W/m}^2$ ). (e,f) Monthly mean gross primary productivity ( $\text{g/m}^2/\text{d}$ ). Solid lines correspond to ambient through-fall conditions, and dotted lines feature 60% through-fall exclusion. Black lines represent model output. Red lines show observational transpiration derived from sap flux (see zqz). PHS is on for (a), (c), and (e). PHS is off for (b), (d), and (f).

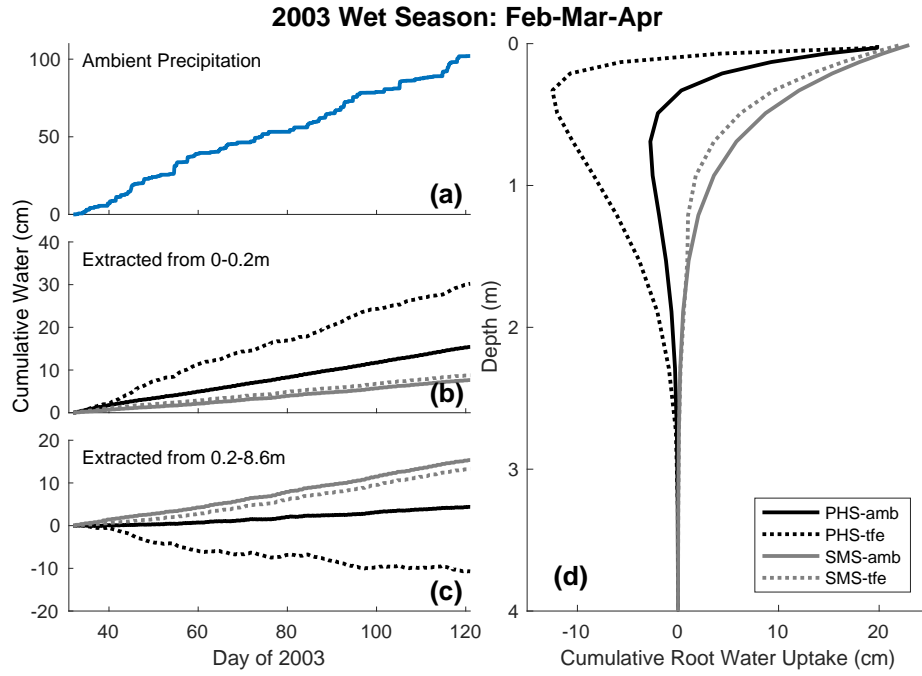


**Figure 8.** Diurnal mean of the Soil Layer 5 conductance, under ambient and TFE conditions during 2003.  
 (a) Time-series of PHS modeled soil-to-root conductance ( $\text{s}^{-1}$ ) from Soil Layer 5 (spanning 20 to 32 centimeters in depth). (b) Time-series of SMS inferred conductance ( $\text{s}^{-1}$ ) also from Soil Layer 5.

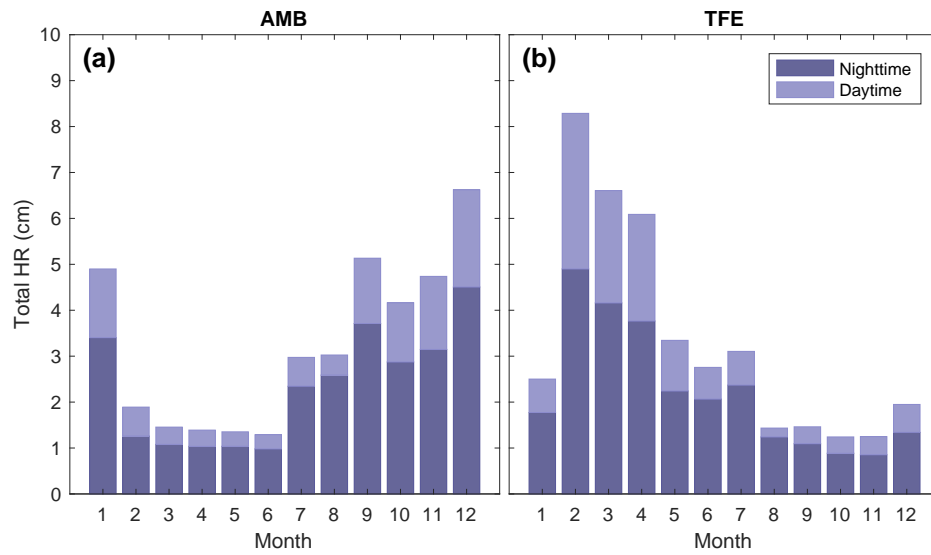




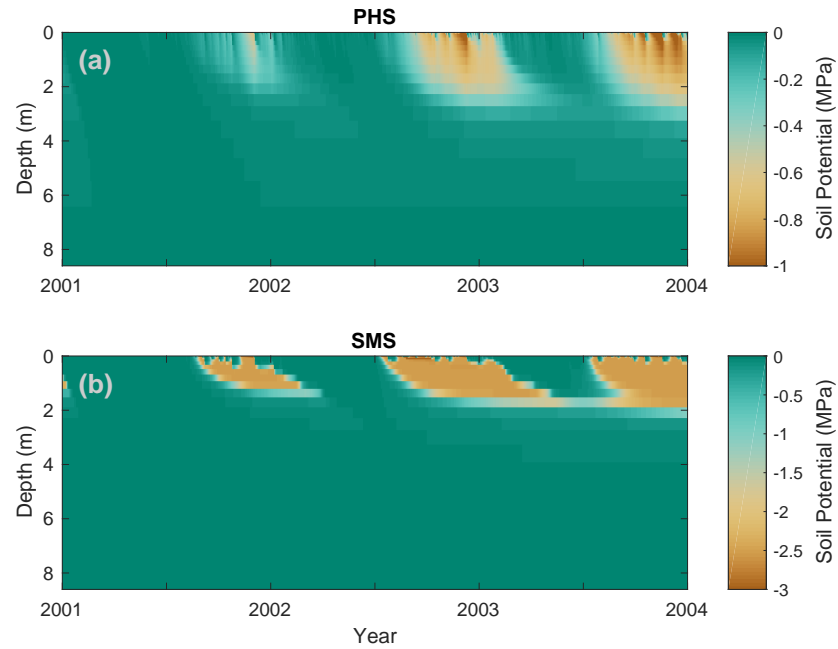
**Figure 9.** 2003 dry season (SON) cumulative root water uptake and precipitation. (a) Cumulative root water uptake with depth across the four simulations. (b,c) Cumulative water uptake over time from above and below 0.2m, respectively. (d) Cumulative precipitation under ambient conditions.



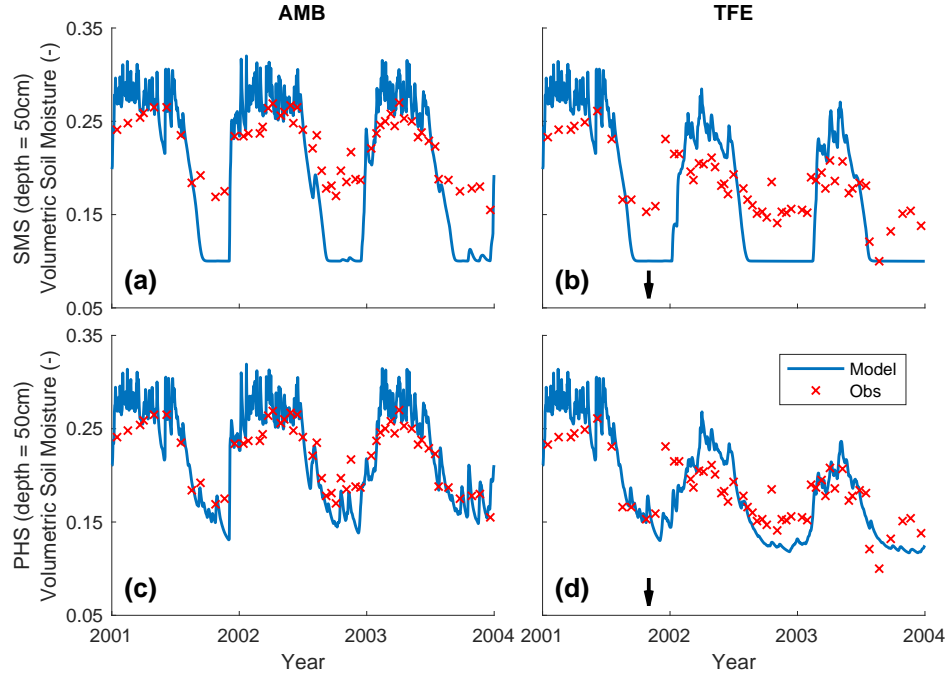
**Figure 10.** 2003 wet season (FMA) cumulative root water uptake and precipitation. (a) Cumulative root water uptake with depth across the four simulations. (b,c) Cumulative water uptake over time from above and below 0.2m, respectively. (d) Cumulative precipitation under ambient conditions.



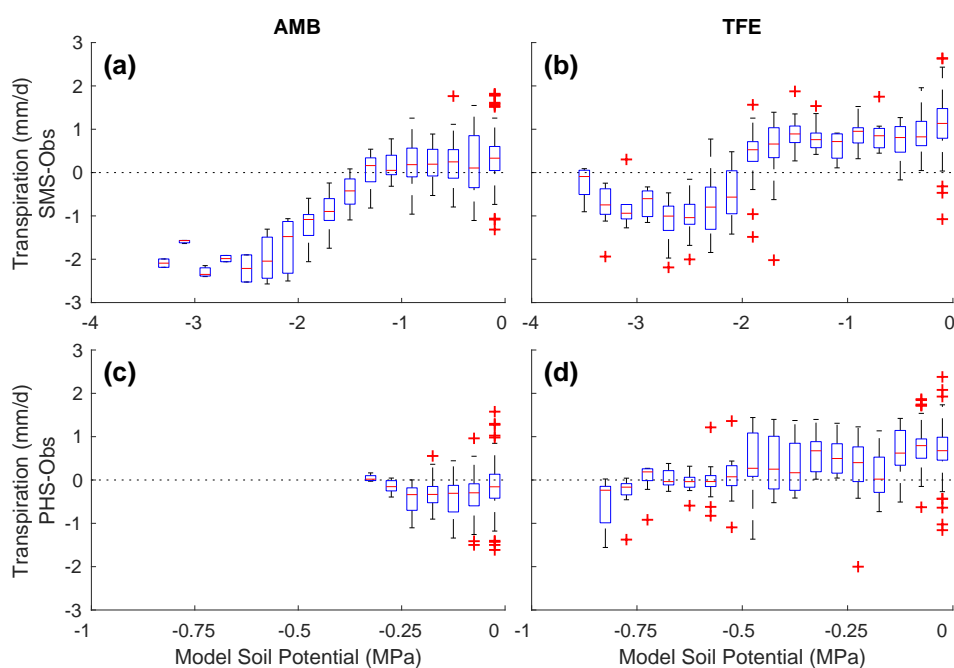
**Figure 11.** Total hydraulic redistribution (cm) by month across in 2003. For (a) ambient through-fall conditions, and (b) 60% through-fall exclusion. Darker shading shows portion of HR at night [6pm,6am), lighter shading shows portion of HR during day [6am,6pm).



**Figure 12.** Vertical profile of soil water potential (MPa) over time under 60% through-fall exclusion, for (a) PHS, and (b) SMS. Note that color axes are different. Figure A.9 duplicates this analysis under ambient conditions. Figure 13 replots this data along with observational soil moisture at 0.5m depth.

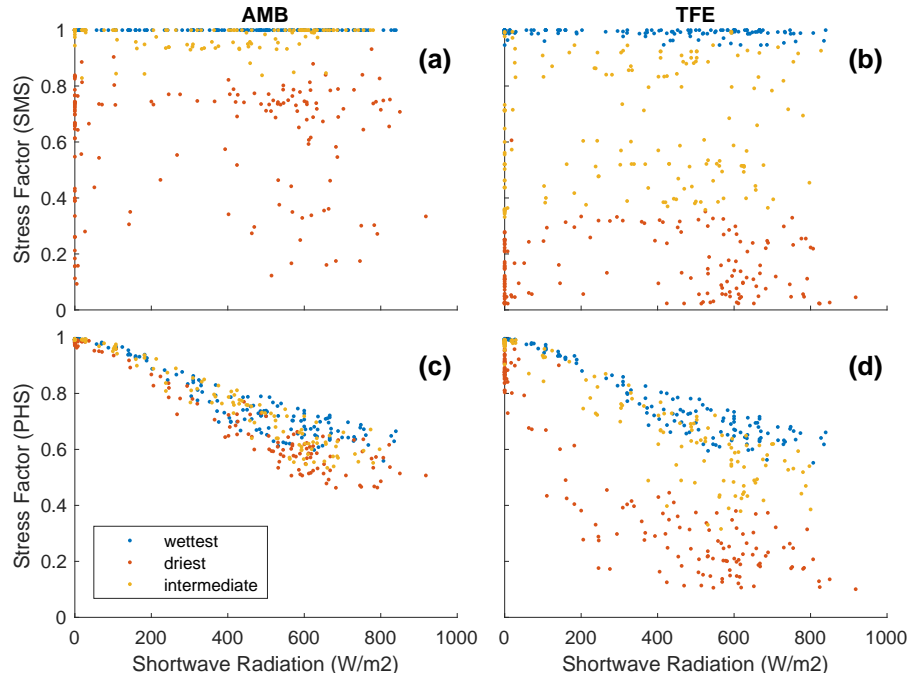


**Figure 13.** Volumetric soil moisture (-) over time under ambient and TFE conditions at depth of 50cm. (a/b) SMS (c/d) PHS Arrows indicate start of TFE. Figure A.10 shows the same plots at 7 other soil depths.



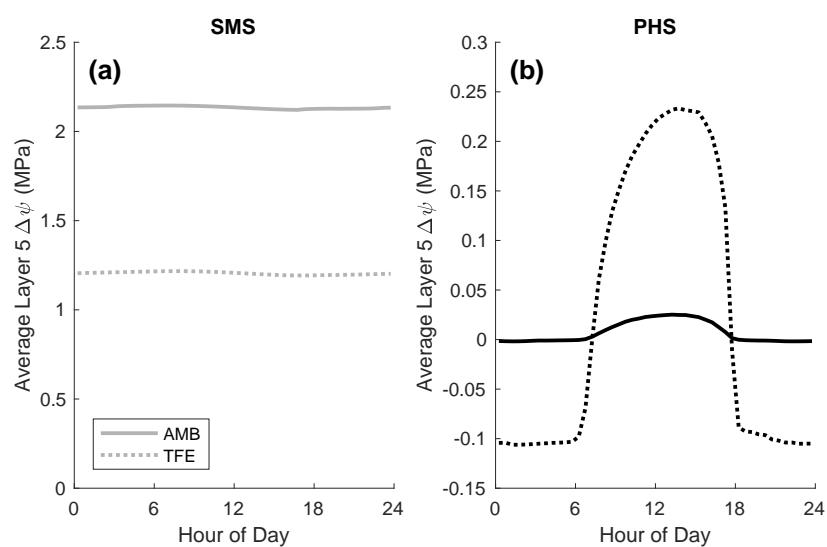
**Figure 14.** Difference between modeled and observed transpiration (mm/d) versus soil potential.

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**A: Supplementary Figures**

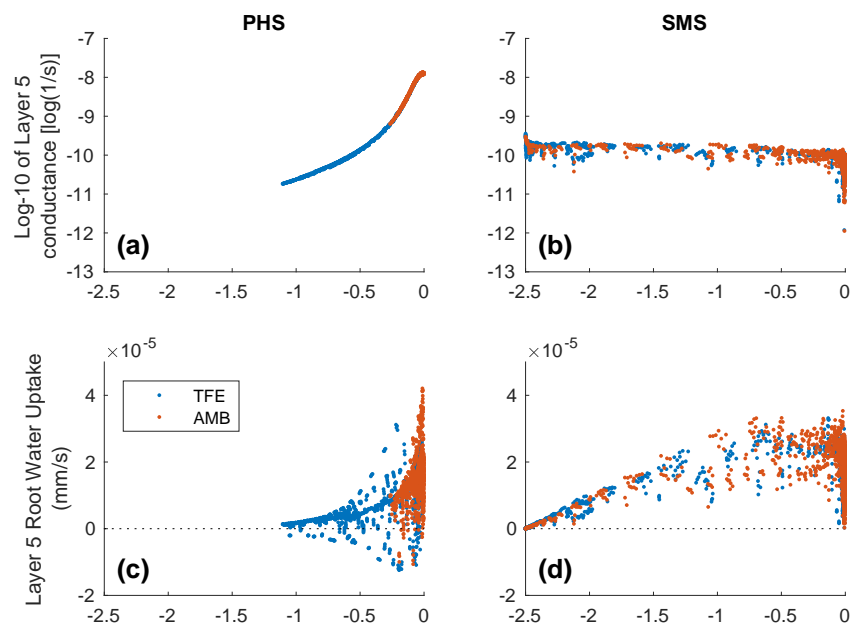
**Figure A.1.** Water stress factor versus downwelling shortwave radiation (2002-2003), for timesteps with VPD between 1 and 1.0559 kPa ( $n=470$ ). VPD is controlled to highlight the relationship with downwelling radiation, the reverse (controlling for radiation) is shown in Figure 5. For SMS (a,b), data are subdivided based on average soil matric potential, weighted by root fraction. For PHS (c,d), data are subdivided based on predawn (5h) root water potential. Blue dots represent the wettest tercile, yellow dots represent the intermediate tercile, and red dots represent the driest tercile.





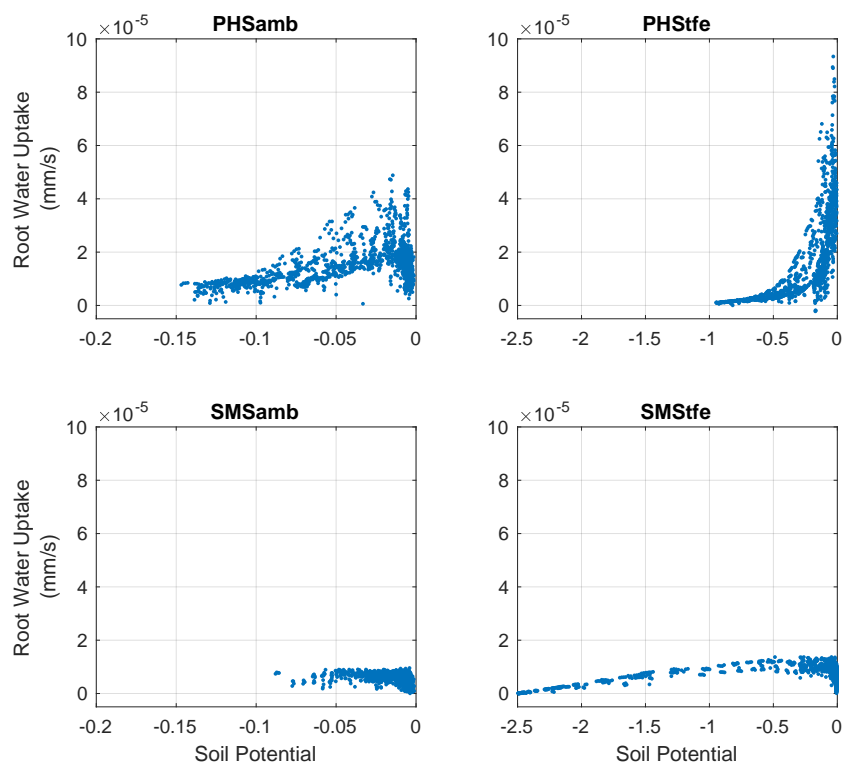
**Figure A.2.** To complement Figure 6

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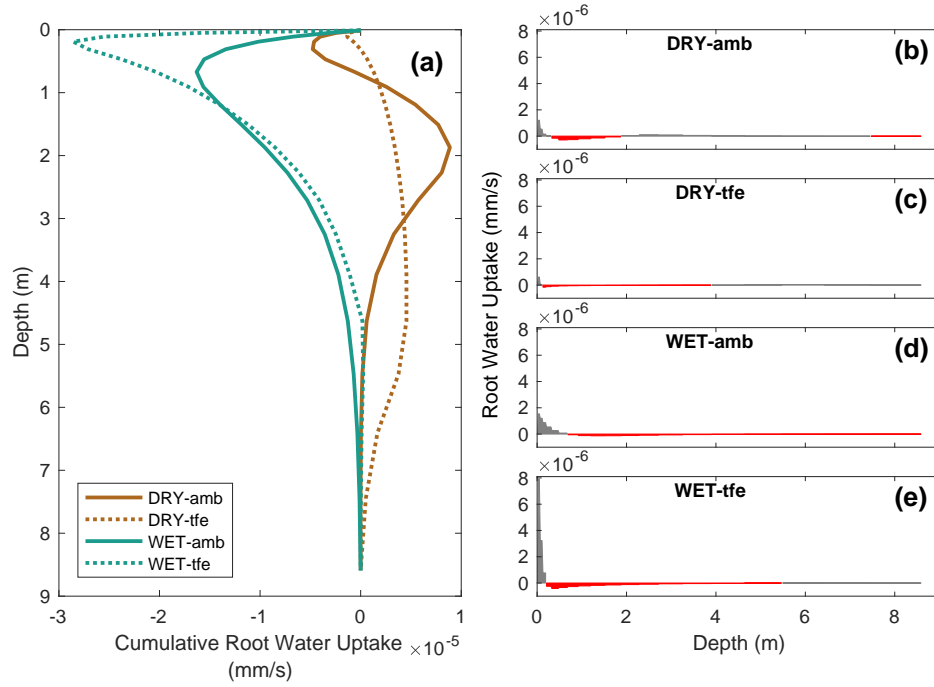
**Figure A.3.** Log of conductance versus soil potential for Soil Layer 3 (2003).

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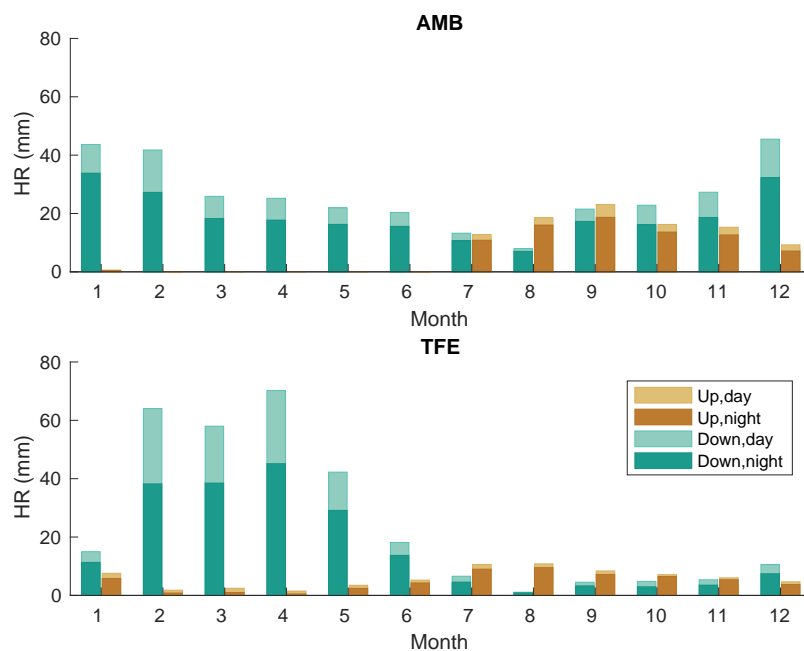


**Figure A.4.** Midday root water uptake versus soil potential for Soil Layer 3 (2003).

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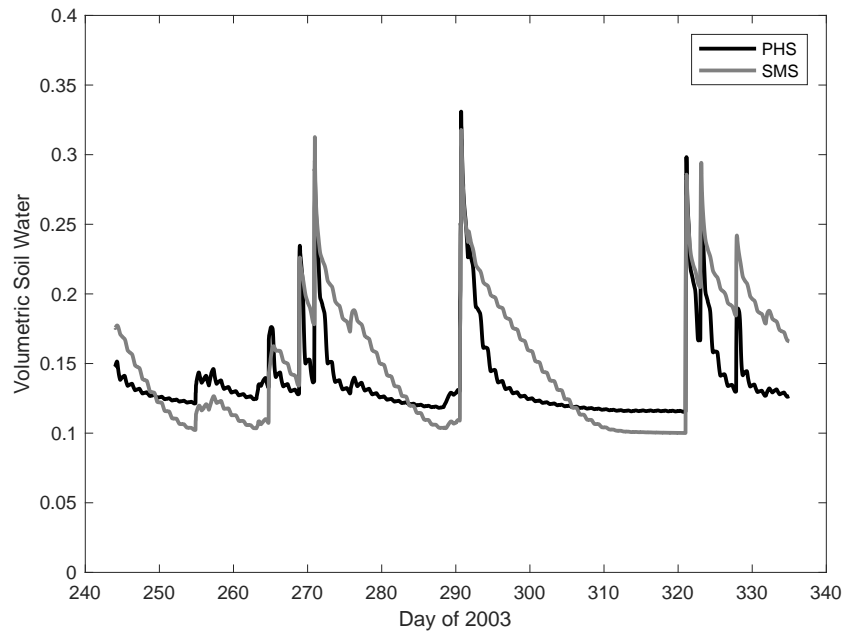


**Figure A.5.** PHS, nighttime (6pm to 6am) average root water uptake profiles with depth. Showing night-time serves to emphasize the profile of hydraulic redistribution. Panel (a) shows cumulative (starting at depth) root water uptake (mm/s) for ambient (solid line) and 60% through-fall exclusion (dotted line) during the wet (FMA, cyan color) and dry (SON, brown color) seasons. Panels (b)-(e) present the information from (a) in non-cumulative form. Note that for panels (b)-(e) negative root water uptake is shaded red, and also that for panel (a), positive slope indicates water uptake, and negative slope indicates water deposited. Note also that SMS is not shown, because hydraulic redistribution is precluded.

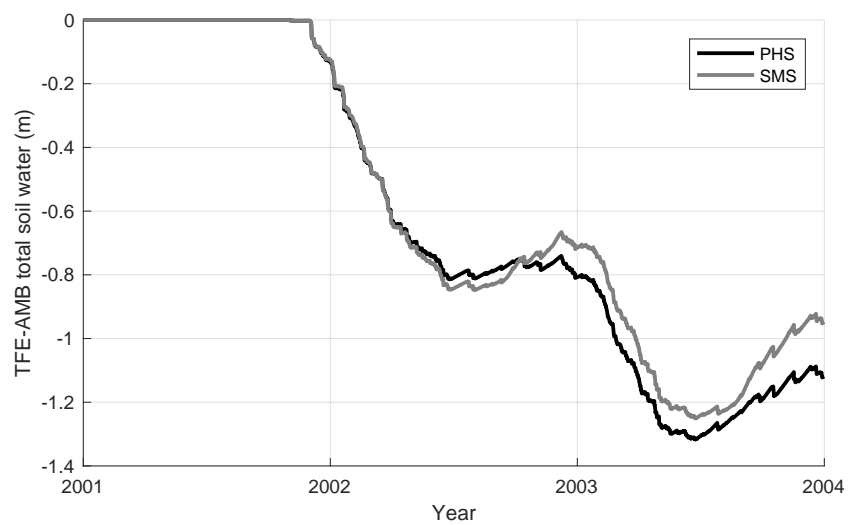


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**Figure A.6.** PHS hydraulic distribution during 2003. Alternative version partitioning by direction.

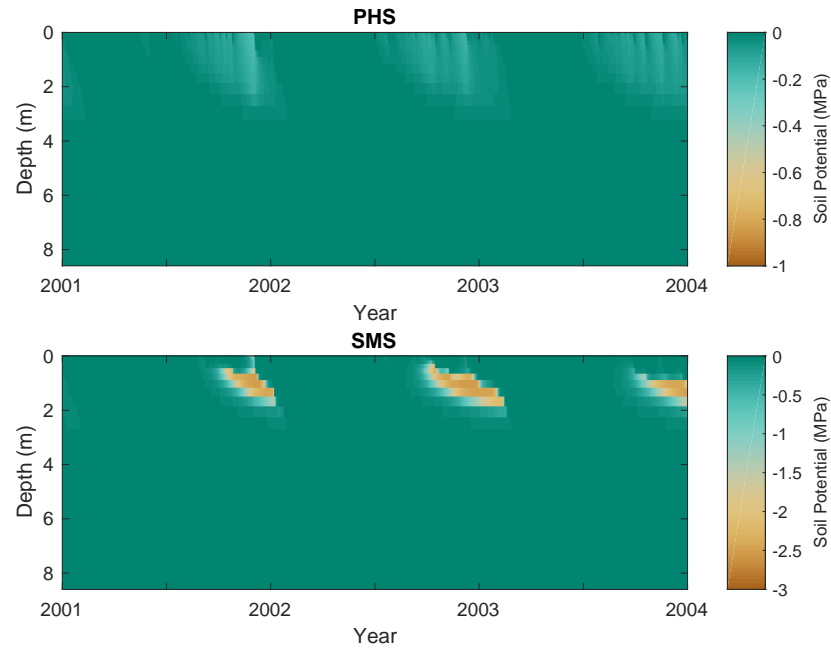


**Figure A.7.** Volumetric soil water content in Soil Layer 2 (which spans 2-6cm in depth), for SON-2003, featuring 60% through-fall exclusion. With PHS (black line), the soil layer can dry out much more quickly after rain events.



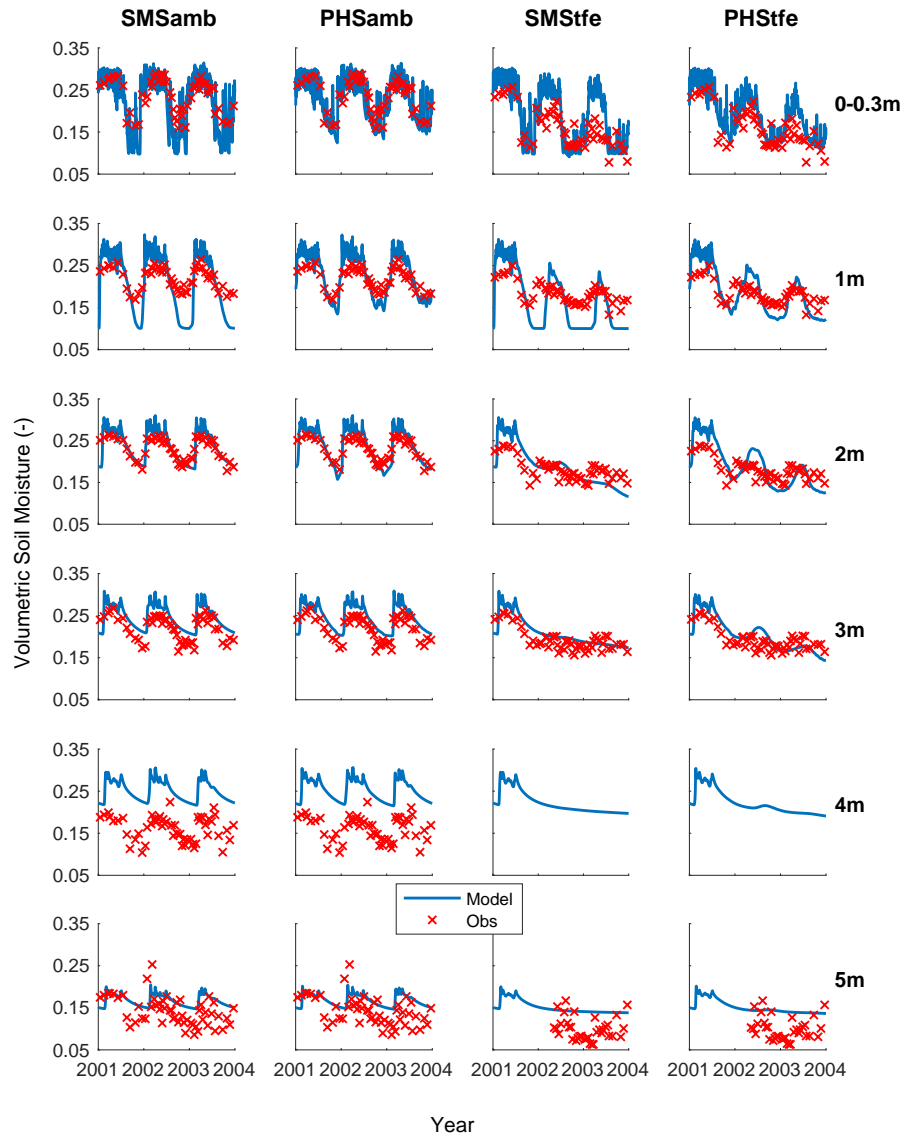
**Figure A.8.** Delta soil water

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**Figure A.9.** Vertical profile of soil water potential (MPa) through time under ambient through-fall conditions, for (a) PHS, and (b) SMS. Note that color axes are different.





**Figure A.10.** Time series of soil moisture by soil layer. Complements Figure 12

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## B: Appendix to Model Description

### B.1 Details of Water Supply

PHS resolves flow across four different segments, soil-to-root, root-to-stem, stem-to-leaf, and leaf-to-transpiration.

Stem-to-leaf. The area bases are sunlit and shaded leaf area, respectively. Note that gravity is assumed negligible here. Likewise there is no length scaling applied to maximum conductance. Therefore the input parameters for  $k_{1,\max}$  should be conductances ( $s^{-1}$ ).

$$\begin{aligned} q_{1a} &= k_1 \cdot \text{LAI-sun} \cdot (\psi_{\text{stem}} - \psi_{\text{sun-leaf}}) \\ q_{1b} &= k_1 \cdot \text{LAI-shade} \cdot (\psi_{\text{stem}} - \psi_{\text{shade-leaf}}) \end{aligned} \quad (\text{B.1})$$

$$k_1 = k_{1,\max} \cdot f(\psi_{\text{stem}}) \quad (\text{B.2})$$

$$f(\psi) = 2 - \left( \frac{\psi}{p_{50}} \right)^{c_k} \quad (\text{B.3})$$

Root-to-stem. The area basis is stem area index. The parameter is maximum stem xylem conductivity ( $K_{2,\max}$ ). Stem conductance ( $k_2$ ) is the result of scaling maximum conductivity by the tree height ( $h$ ) and applying loss relative to maximum conductance via the vulnerability curve  $f(\psi_{\text{root}})$ .

$$q_2 = k_2 \cdot \text{SAI} \cdot (\psi_{\text{root}} - \psi_{\text{stem}} - \rho g h) \quad (\text{B.4})$$

$$k_2 = \frac{K_{2,\max}}{h} \cdot f(\psi_{\text{root}}) \quad (\text{B.5})$$

Soil-to-root. Area basis is RAI in soil layer  $i$ , which is based on the layer root fraction times the total root area. Total root area we have as the summed stem and leaf area indices multiplied by a relative root area parameter ( $f_{\text{root}}$ ). The vertical root distribution is defined by the layer root fraction ( $r_i$ ), which follows a one-parameter (by PFT) power law decay following *Jackson et al.* [1996].

$$q_{3,i} = k_{3,i} \cdot \text{RAI}_i \cdot (\psi_{\text{soil},i} - \psi_{\text{root}} - \rho g z_i) \quad (\text{B.6})$$

$$\text{RAI}_i = f_{\text{root}} \cdot (\text{SAI} + \text{LAI}) \cdot r_i \quad (\text{B.7})$$

$$k_{3,i} = \frac{k_{r,i} + k_{s,i}}{k_{r,i} \cdot k_{s,i}} \quad (\text{B.8})$$

$$k_{r,i} = \frac{K_{r,\max}}{l_i} f(\psi_{\text{soil},i}) \quad (\text{B.9})$$

$$l_i = z_i + x \quad (\text{B.10})$$

$$k_{s,i} = \frac{K_{s,i}}{d} \quad (\text{B.11})$$

The conductance  $k_{3,i}$  reflects two resistors in series, from soil-to-root ( $k_{s,i}$ ) and through the root tissue ( $k_{r,i}$ ). The root tissue conductance is attenuated via the vulnerability curve framework. The input parameter is maximum root xylem conductivity, on the basis of RAI as defined above. The root conductivity is scaled by the conducting length, which is estimated as the sum of soil layer depth ( $z_i$ ) and average lateral extent ( $x$ , static parameter). The soil conductivity  $K_{s,i}$  is calculated from the layer soil matric potential ( $\psi_s$ ) and soil properties following *Clapp and Hornberger* [1978] as described in *Oleson et al.* [2013]. The soil conductance ( $k_{s,i}$ ) is the result of scaling the conductivity by  $d$ , the distance between roots estimated following *Williams et al.* [1996] and *Bonan et al.* [2014]

The challenge here is obviously getting your head around all the parameters.

## B.2 Details of Water Demand

## B.3 Details of Solution

The continuity of water flow through the system yields four equations

$$\begin{aligned}
 E_{sun} &= q_{1a} \\
 E_{shade} &= q_{1b} \\
 q_{1a} + q_{1b} &= q_2 \\
 q_2 &= \sum_{i=1}^{nlevsoi} q_{3,i}
 \end{aligned} \tag{B.12}$$

We seek the set of vegetation water potential values (four unknowns),

$$\psi = \begin{bmatrix} \psi_{sunleaf} \\ \psi_{shadeleaf} \\ \psi_{stem} \\ \psi_{root} \end{bmatrix} \tag{B.13}$$

that satisfies these equations, as forced by the soil moisture and atmospheric state.

Each flux on the schematic can be represented in terms of the relevant water potentials.

Defining the transpiration fluxes:

$$\begin{aligned}
 E_{sun} &= E_{sun,max} \cdot 2^{-\left(\frac{\psi_{sunleaf}}{p50_e}\right)^{c_k}} \\
 E_{shade} &= E_{shade,max} \cdot 2^{-\left(\frac{\psi_{shadeleaf}}{p50_e}\right)^{c_k}}
 \end{aligned} \tag{B.14}$$

Defining the water supply fluxes:

$$\begin{aligned}
 q_{1a} &= k_{1a,max} \cdot 2^{-\left(\frac{\psi_{stem}}{p50_1}\right)^{c_k}} \cdot LAI_{sun} \cdot (\psi_{stem} - \psi_{sunleaf}) \\
 q_{1b} &= k_{1b,max} \cdot 2^{-\left(\frac{\psi_{stem}}{p50_1}\right)^{c_k}} \cdot LAI_{shade} \cdot (\psi_{stem} - \psi_{shadeleaf}) \\
 q_2 &= \frac{k_{2,max}}{z_2} \cdot 2^{-\left(\frac{\psi_{root}}{p50_2}\right)^{c_k}} \cdot SAI \cdot (\psi_{root} - \psi_{stem} - \Delta\psi_z) \\
 q_{soil} &= \sum_{i=1}^{nlevsoi} q_{3,i} = \sum_{i=1}^{nlevsoi} k_{3,i} \cdot RAI \cdot (\psi_{soil,i} - \psi_{root} + \Delta\psi_{z,i})
 \end{aligned} \tag{B.15}$$

We're looking to find the vector  $\psi$  that fits with soil and atmospheric forcings while satisfying water flow continuity. Due to the model non-linearity, we use a linearized explicit approach, iterating with Newton's method. The initial guess is the solution for  $\psi$  (vector) from the previous time step. The general framework, from iteration  $m$  to  $m + 1$  is:

$$\begin{aligned}
 q^{m+1} &= q^m + \frac{\delta q}{\delta \psi} \Delta\psi \\
 \psi^{m+1} &= \psi^m + \Delta\psi
 \end{aligned} \tag{B.16}$$

So for our first flux balance equation, at iteration  $m + 1$ , we have:

$$E_{sun}^{m+1} = q_{1a}^{m+1} \quad (B.17)$$

Which can be linearized to:

$$E_{sun}^m + \frac{\delta E_{sun}}{\delta \psi} \Delta \psi = q_{1a}^m + \frac{\delta q_{1a}}{\delta \psi} \Delta \psi \quad (B.18)$$

And rearranged to be:

$$\frac{\delta q_{1a}}{\delta \psi} \Delta \psi - \frac{\delta E_{sun}}{\delta \psi} \Delta \psi = E_{sun}^m - q_{1a}^m \quad (B.19)$$

And for the other 3 flux balance equations:

$$\begin{aligned} \frac{\delta q_{1b}}{\delta \psi} \Delta \psi - \frac{\delta E_{sha}}{\delta \psi} \Delta \psi &= E_{sha}^m - q_{1b}^m \\ \frac{\delta q_2}{\delta \psi} \Delta \psi - \frac{\delta q_{1a}}{\delta \psi} \Delta \psi - \frac{\delta q_{1b}}{\delta \psi} \Delta \psi &= q_{1a}^m + q_{1b}^m - q_2^m \\ \frac{\delta q_{soil}}{\delta \psi} \Delta \psi - \frac{\delta q_2}{\delta \psi} \Delta \psi &= q_2^m - q_{soil}^m \end{aligned} \quad (B.20)$$

Putting all four together in matrix form:

$$\begin{bmatrix} \frac{\delta q_{1a}}{\delta \psi} - \frac{\delta E_{sun}}{\delta \psi} \\ \frac{\delta q_{1b}}{\delta \psi} - \frac{\delta E_{sha}}{\delta \psi} \\ \frac{\delta q_2}{\delta \psi} - \frac{\delta q_{1a}}{\delta \psi} - \frac{\delta q_{1b}}{\delta \psi} \\ \frac{\delta q_{soil}}{\delta \psi} - \frac{\delta q_2}{\delta \psi} \end{bmatrix} \Delta \psi = \begin{bmatrix} E_{sun}^m - q_{1a}^m \\ E_{sha}^m - q_{1b}^m \\ q_{1a}^m + q_{1b}^m - q_2^m \\ q_2^m - q_{soil}^m \end{bmatrix} \quad (B.21)$$

Now to expand the left-hand side, from vector  $\psi$  to the four distinct plant water potential nodes, noting that many derivatives are zero (e.g.  $\frac{\delta E_{sun}}{\delta \psi_{sha}} = 0$ )

Introducing the notation:  $A \Delta \psi = b$

$$\Delta \psi = \begin{bmatrix} \Delta \psi_{sunleaf} \\ \Delta \psi_{shadeleaf} \\ \Delta \psi_{stem} \\ \Delta \psi_{root} \end{bmatrix} \quad (B.22)$$

$$A = \begin{bmatrix} \frac{\delta q_{1a}}{\delta \psi_{sun}} - \frac{\delta E_{sun}}{\delta \psi_{sun}} & 0 & \frac{\delta q_{1a}}{\delta \psi_{stem}} & 0 \\ 0 & \frac{\delta q_{1b}}{\delta \psi_{sha}} - \frac{\delta E_{sha}}{\delta \psi_{sha}} & \frac{\delta q_{1b}}{\delta \psi_{stem}} & 0 \\ -\frac{\delta q_{1a}}{\delta \psi_{sun}} & -\frac{\delta q_{1b}}{\delta \psi_{sha}} & \frac{\delta q_2}{\delta \psi_{stem}} - \frac{\delta q_{1a}}{\delta \psi_{stem}} - \frac{\delta q_{1b}}{\delta \psi_{stem}} & \frac{\delta q_2}{\delta \psi_{root}} \\ 0 & 0 & -\frac{\delta q_2}{\delta \psi_{stem}} & \frac{\delta q_{soil}}{\delta \psi_{root}} - \frac{\delta q_2}{\delta \psi_{root}} \end{bmatrix} \quad (B.23)$$

$$b = \begin{bmatrix} E_{sun}^m - q_{b1}^m \\ E_{sha}^m - q_{b2}^m \\ q_{b1}^m + q_{b2}^m - q_{stem}^m \\ q_{stem}^m - q_{soil}^m \end{bmatrix} \quad (B.24)$$

Now we compute all the entries for  $A$  and  $b$  based on the soil moisture and maximum transpiration forcings and can solve to find:

$$\Delta\psi = A^{-1}b \quad (B.25)$$

$$\psi_{m+1} = \psi_m + \Delta\psi \quad (B.26)$$

We iterate until  $b \rightarrow 0$ , signifying water flux balance through the system. The result is a final set of water potentials ( $\psi_{root}$ ,  $\psi_{xylem}$ ,  $\psi_{shadeleaf}$ ,  $\psi_{sunleaf}$ ) satisfying non-divergent water flux through the system. The magnitude of the water flux is driven by soil matric potential and unstressed ( $\beta_t = 1$ ) transpiration.

We use the transpiration solution (corresponding to the final solution for  $\psi$ ) to compute stomatal conductance. The stomatal conductance is then used to compute  $\beta_t$ .

$$\beta_{t,sun} = \frac{g_{s,sun}}{g_{s,sun,\beta_t=1}} \quad (B.27)$$

$$\beta_{t,shade} = \frac{g_{s,shade}}{g_{s,shade,\beta_t=1}} \quad (B.28)$$

The  $\beta_t$  values are used in the Photosynthesis module (see section 2.1) to apply water stress. The solution for  $\psi$  is saved as a new variable (vegetation water potential) and is indicative of plant water status. The soil-to-root fluxes ( $q_{3,1}$ ,  $q_{3,2}$ , ...,  $q_{3,n}$ ) are used as the soil transpiration sink in the Richards' equation subsurface flow equations.

Furthermore several simplifications were made that decrease the numerical complexity. For the purposes of the PHS solution, soil potentials are assumed constant during each timestep. Plant tissue water storage (capacitance) is not represented, whereby the solution does not depend on the previous timestep and has no time derivatives.

## Acknowledgments

= enter acknowledgments here =

Pierre: Text I removed While there are disagreements about soil moisture trends globally [Dai, 2013; Sheffield *et al.*, 2012], Amazonia has experienced and a lengthening dry season [Fu *et al.*, 2013] and faces projections of increasing frequency of extreme El Niño events [Cai *et al.*, 2014]

## References

- Alistair, R., M. B. E., D. J. S., B. Gordon, C. Susanne, D. M. C., K. Jens, L. A. D. B., M. L. M., N. ÁIJlo, P. I. Colin, S. S. P., S. Stephen, W. D. A., and Z. Štůnke (2017), A roadmap for improving the representation of photosynthesis in earth system models, *New Phytologist*, 213(1), 22–42, doi:10.1111/nph.14283.
- Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. T. Hogg, P. Gonzalez, R. Fensham,

- 1095 Z. Zhang, J. Castro, N. Demidova, J.-H. Lim, G. Allard, S. W. Running, A. Semerci, and  
1096 N. Cobb (2010), A global overview of drought and heat-induced tree mortality reveals  
1097 emerging climate change risks for forests, *Forest Ecology and Management*, 259(4), 660 –  
1098 684, doi:https://doi.org/10.1016/j.foreco.2009.09.001.
- 1099 Anderegg, W. R. L. (2015a), Spatial and temporal variation in plant hydraulic traits and their  
1100 relevance for climate change impacts on vegetation, *New Phytologist*, 205(3), 1008–1014,  
1101 doi:10.1111/nph.12907.
- 1102 Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg (2013a), Consequences of  
1103 widespread tree mortality triggered by drought and temperature stress, *Nature Climate*  
1104 *Change*, 3(1), 30–36.
- 1105 Anderegg, W. R. L., L. Plavcová, L. D. L. Anderegg, U. G. Hacke, J. A. Berry, and C. B.  
1106 Field (2013b), Drought’s legacy: multiyear hydraulic deterioration underlies widespread  
1107 aspen forest die-off and portends increased future risk, *Global Change Biology*, 19(4),  
1108 1188–1196, doi:10.1111/gcb.12100.
- 1109 Anderegg, W. R. L., C. Schwalm, F. Biondi, J. J. Camarero, G. Koch, M. Litvak, K. Ogle,  
1110 J. D. Shaw, E. Shevliakova, A. P. Williams, A. Wolf, E. Ziaco, and S. Pacala (2015b), Per-  
1111 vasive drought legacies in forest ecosystems and their implications for carbon cycle mod-  
1112 els, *Science*, 349(6247), 528–532, doi:10.1126/science.aab1833.
- 1113 Anderegg, W. R. L., A. Wolf, A. Arango-Velez, B. Choat, D. J. Chmura, S. Jansen, T. Kolb,  
1114 S. Li, F. Meinzer, P. Pita, V. Resco de Dios, J. S. Sperry, B. T. Wolfe, and S. Pacala (2017),  
1115 Plant water potential improves prediction of empirical stomatal models, *PLOS ONE*,  
1116 12(10), 1–17, doi:10.1371/journal.pone.0185481.
- 1117 Bartlett, M. K., T. Klein, S. Jansen, B. Choat, and L. Sack (2016), The correlations and se-  
1118 quence of plant stomatal, hydraulic, and wilting responses to drought, *Proceedings of the*  
1119 *National Academy of Sciences*, 113(46), 13,098–13,103, doi:10.1073/pnas.1604088113.
- 1120 Bohrer, G., M. Hashem, L. T. A., D. Darren, A. Roni, P. Davide, O. Ram, and K. G. G.  
1121 (2005), Finite element tree crown hydrodynamics model (fetch) using porous media flow  
1122 within branching elements: A new representation of tree hydrodynamics, *Water Resources*  
1123 *Research*, 41(11), doi:10.1029/2005WR004181.
- 1124 Bonan, G. B., P. J. Lawrence, K. W. Oleson, S. Levis, M. Jung, M. Reichstein, D. M.  
1125 Lawrence, and S. C. Swenson (2011), Improving canopy processes in the Commu-  
1126 nity Land Model version 4 (CLM4) using global flux fields empirically inferred from  
1127 FLUXNET data, *Journal of Geophysical Research*, 116, doi:10.1029/2010JG001593.
- 1128 Bonan, G. B., M. Williams, R. A. Fisher, and K. W. Oleson (2014), Modeling stomatal con-  
1129 ductance in the earth system: linking leaf water-use efficiency and water transport along  
1130 the soil-plant-atmosphere continuum, *Geoscientific Model Development*, 7(5), 2193–2222,  
1131 doi:10.5194/gmd-7-2193-2014.
- 1132 Boyer, J. S. (1967), Leaf water potentials measured with a pressure chamber, *Plant Physiol-*  
1133 *ogy*, 42(1), 133–137, doi:10.1104/pp.42.1.133.
- 1134 Brooks, J. R., F. C. Meinzer, J. M. Warren, J.-C. Domec, and R. Coulombe (2006), Hydraulic  
1135 redistribution in a douglas-fir forest: lessons from system manipulations, *Plant, Cell &*  
1136 *Environment*, 29(1), 138–150, doi:10.1111/j.1365-3040.2005.01409.x.
- 1137 Burgess, S. S. O., M. A. Adams, N. C. Turner, and C. K. Ong (1998), The redistribution of  
1138 soil water by tree root systems, *Oecologia*, 115(3), 306–311, doi:10.1007/s004420050521.
- 1139 Cai, W., S. Borlace, M. Lengaigne, P. Van Rensch, M. Collins, G. Vecchi, A. Timmermann,  
1140 A. Santoso, M. J. Mcphaden, L. Wu, M. H. England, G. Wang, E. Guilyardi, and F.-f. Jin  
1141 (2014), Increasing frequency of extreme El Niño events due to greenhouse warming, *Na-*  
1142 *ture Climate Change*, 4(2), 111–116.
- 1143 Celia, M. A., E. T. Bouloutas, and R. L. Zarba (1990), A general mass-conservative numer-  
1144 ical solution for the unsaturated flow equation, *Water Resources Research*, 26(7), 1483–  
1145 1496, doi:10.1029/WR026i007p01483.
- 1146 Choat, B., S. Jansen, T. J. Brodribb, H. Cochard, S. Delzon, R. Bhaskar, S. J. Bucci, T. S.  
1147 Feild, S. M. Gleason, U. G. Hacke, A. L. Jacobsen, F. Lens, H. Maherali, J. Martínez-  
1148 Vilalta, S. Mayr, M. Mencuccini, P. J. Mitchell, A. Nardini, J. Pittermann, R. B. Pratt, J. S.

- Sperry, M. Westoby, I. J. Wright, and A. E. Zanne (2012), Global convergence in the vulnerability of forests to drought, *Nature*, 491(7426), 752–5.
- Christoffersen, B. O., M. Gloor, S. Fauset, N. M. Fyllas, D. R. Galbraith, T. R. Baker, B. Kruijt, L. Rowland, R. A. Fisher, O. J. Binks, S. Sevanto, C. Xu, S. Jansen, B. Choat, M. Mencuccini, N. G. McDowell, and P. Meir (2016), Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (tfs v.1-hydro), *Geoscientific Model Development*, 9(11), 4227–4255, doi:10.5194/gmd-9-4227-2016.
- Clapp, R. B., and G. M. Hornberger (1978), Empirical equations for some soil hydraulic properties, *Water Resources Research*, 14(4), 601–604, doi:10.1029/WR014i004p00601.
- Collatz, G., J. Ball, C. Grivet, and J. A. Berry (1991), Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer, *Agricultural and Forest Meteorology*, 54(2), 107 – 136, doi: [http://dx.doi.org/10.1016/0168-1923\(91\)90002-8](http://dx.doi.org/10.1016/0168-1923(91)90002-8).
- da Costa, A. C., D. B. Metcalfe, C. E. Doughty, A. A. de Oliveira, G. F. Neto, M. C. da Costa, J. de Athaydes Silva Junior, L. E. Aragão, S. Almeida, D. R. Galbraith, L. M. Rowland, P. Meir, and Y. Malhi (2014), Ecosystem respiration and net primary productivity after 8–10 years of experimental through-fall reduction in an eastern Amazon forest, *Plant Ecology & Diversity*, 7(1–2), 7–24, doi:10.1080/17550874.2013.798366.
- da Costa, A. C. L., D. Galbraith, S. Almeida, B. Takeshi, T. Portela, M. da Costa, J. ao de Athaydes Silva Junior, A. P. Braga, P. H. L. de Gonçalves, A. A. de Oliveira, R. Fisher, O. L. Phillips, D. B. Metcalfe, P. Levy, and P. Meir (2010), Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern amazonian rainforest, *The New Phytologist*, 187(3), 579–591.
- Dai, A. (2013), Increasing drought under global warming in observations and models, *Nature Climate Change*, 3(1), 52–58.
- Dai, Y., R. E. Dickinson, and Y.-P. Wang (2004), A two-big-leaf model for canopy temperature, photosynthesis, and stomatal conductance, *Journal of Climate*, 17(12), 2281–2299, doi:10.1175/1520-0442(2004)017<2281:ATMFCT>2.0.CO;2.
- De Kauwe, M. G., J. Kala, Y.-S. Lin, A. J. Pitman, B. E. Medlyn, R. A. Duursma, G. Abramowitz, Y.-P. Wang, and D. G. Miralles (2015), A test of an optimal stomatal conductance scheme within the CABLE land surface model, *Geoscientific Model Development*, 8(2), 431–452, doi:10.5194/gmd-8-431-2015.
- De Kauwe, M. G., B. E. Medlyn, J. Knauer, and C. A. Williams (2017), Ideas and perspectives: how coupled is the vegetation to the boundary layer?, *Biogeosciences*, 14(19), 4435–4453, doi:10.5194/bg-14-4435-2017.
- Domec, J.-C., J. S. King, A. Noormets, E. Treasure, M. J. Gavazzi, G. Sun, and S. G. McNulty (2010), Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange, *The New Phytologist*, 187(1), 171–183, doi:10.1111/j.1469-8137.2010.03245.x.
- Drake, J., S. Power, R. Duursma, B. Medlyn, M. Aspinwall, B. Choat, D. Creek, D. Eamus, C. Maier, S. Pfautsch, R. Smith, M. Tjoelker, and D. Tissue (2017), Stomatal and non-stomatal limitations of photosynthesis for four tree species under drought: A comparison of model formulations, *Agricultural and Forest Meteorology*, 247, 454 – 466, doi: <https://doi.org/10.1016/j.agrformet.2017.08.026>.
- Egea, G., A. Verhoef, and P. L. Vidale (2011), Towards an improved and more flexible representation of water stress in coupled photosynthesis-stomatal conductance models, *Agricultural and Forest Meteorology*, 151(10), 1370 – 1384, doi: <https://doi.org/10.1016/j.agrformet.2011.05.019>.
- Entekhabi, D., E. G. Njoku, P. E. O’Neill, K. H. Kellogg, W. T. Crow, W. N. Edelstein, J. K. Entin, S. D. Goodman, T. J. Jackson, J. Johnson, J. Kimball, J. R. Piepmeier, R. D. Koster, N. Martin, K. C. McDonald, M. Moghaddam, S. Moran, R. Reichle, J. C. Shi, M. W. Spencer, S. W. Thurman, L. Tsang, and J. V. Zyl (2010), The soil moisture active passive (smap) mission, *Proceedings of the IEEE*, 98(5), 704–716, doi: 10.1109/JPROC.2010.2043918.



- Epila, J., N. J. De Baerdemaeker, L. L. Vergeynst, W. H. Maes, H. Beeckman, and K. Steppe (2017), Capacitive water release and internal leaf water relocation delay drought-induced cavitation in African *Maesopsis eminii*, *Tree Physiology*, 37(4), 481–490, doi: 10.1093/treephys/tpw128.
- Farquhar, G. D., S. von Caemmerer, and J. A. Berry (1980), A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species, *Planta*, 149(1), 78–90, doi: 10.1007/BF00386231.
- Ficklin, D. L., and K. A. Novick (2017), Historic and projected changes in vapor pressure deficit suggest a continental-scale drying of the United States atmosphere, *Journal of Geophysical Research: Atmospheres*, 122(4), 2061–2079, doi:10.1002/2016JD025855.
- Fisher, R. A., M. Williams, R. L. Do Vale, A. L. Da Costa, and P. Meir (2006), Evidence from Amazonian forests is consistent with isohydric control of leaf water potential, *Plant, Cell & Environment*, 29(2), 151–165, doi:10.1111/j.1365-3040.2005.01407.x.
- Fisher, R. A., M. Williams, A. L. D. Costa, Y. Malhi, R. F. D. Costa, S. Almeida, and P. Meir (2007), The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment, *Global Change Biology*, 13(11), 2361–2378, doi:10.1111/j.1365-2486.2007.01417.x.
- Fisher, R. A., M. Williams, M. de Lourdes Ruivo, A. L. de Costa, and P. Meir (2008), Evaluating climatic and soil water controls on evapotranspiration at two Amazonian rainforest sites, *Agricultural and Forest Meteorology*, 148(6), 850 – 861, doi: <https://doi.org/10.1016/j.agrformet.2007.12.001>.
- Flexas, J., J. Bota, F. Loreto, G. Cornic, and T. D. Sharkey (2004), Diffusive and metabolic limitations to photosynthesis under drought and salinity in c3 plants, *Plant Biology*, 6(3), 269–279, doi:10.1055/s-2004-820867.
- Flexas, J., M. Ribas-Carbó, J. Bota, J. Galmés, M. Henkle, S. Martínez-Cañellas, and H. Medrano (2006), Decreased rubisco activity during water stress is not induced by decreased relative water content but related to conditions of low stomatal conductance and chloroplast CO<sub>2</sub> concentration, *New Phytologist*, 172(1), 73–82, doi:10.1111/j.1469-8137.2006.01794.x.
- Franks, P. J., P. L. Drake, and R. H. Froend (2007), Anisohydric but isohydrodynamic: seasonally constant plant water potential gradient explained by a stomatal control mechanism incorporating variable plant hydraulic conductance, *Plant, Cell & Environment*, 30(1), 19–30, doi:10.1111/j.1365-3040.2006.01600.x.
- Friedlingstein, P., M. Meinshausen, V. K. Arora, C. D. Jones, A. Anav, S. K. Liddicoat, and R. Knutti (2014), Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks, *Journal of Climate*, 27(2), 511–526.
- Fu, R., L. Yin, W. Li, P. A. Arias, R. E. Dickinson, L. Huang, S. Chakraborty, K. Fernandes, B. Liebmann, R. Fisher, and R. B. Myneni (2013), Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection, *Proceedings of the National Academy of Sciences of the United States of America*, 110(45), 18,110–18,115.
- Gentine, P., M. Guérin, M. Uriarte, N. G. McDowell, and W. T. Pockman (2016), An allometry-based model of the survival strategies of hydraulic failure and carbon starvation, *Ecohydrology*, 9(3), 529–546, doi:10.1002/eco.1654.
- Grant, J., J.-P. Wigneron, R. D. Jeu, H. Lawrence, A. Mialon, P. Richaume, A. A. Bitar, M. Drusch, M. van Marle, and Y. Kerr (2016), Comparison of SMOS and AMSR-E vegetation optical depth to four MODIS-based vegetation indices, *Remote Sensing of Environment*, 172, 87 – 100, doi:<https://doi.org/10.1016/j.rse.2015.10.021>.
- Green, J. K., A. G. Konings, S. H. Alemohammad, J. Berry, D. Entekhabi, J. Kolassa, J.-E. Lee, and P. Gentine (2017), Regionally strong feedbacks between the atmosphere and terrestrial biosphere, *Nature Geoscience*, 10(6), 410–414, doi:10.1038/ngeo2957.
- Harley, P. C., R. B. Thomas, J. F. Reynolds, and B. R. Strain (1992), Modelling photosynthesis of cotton grown in elevated co<sub>2</sub>, *Plant Cell Environment*, 15(3), 271–282, doi: 10.1111/j.1365-3040.1992.tb00974.x.



- Holbrook, N. M., E. T. Ahrens, M. J. Burns, and M. A. Zwieniecki (2001), In vivo observation of cavitation and embolism repair using magnetic resonance imaging, *Plant Physiology*, 126(1), 27–31, doi:10.1104/pp.126.1.27.
- Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze (1996), A global analysis of root distributions for terrestrial biomes, *Oecologia*, 108(3), 389–411, doi:10.1007/BF00333714.
- Joetzjer, E., C. Delire, H. Douville, P. Ciais, B. Decharme, R. Fisher, B. Christoffersen, J. C. Calvet, A. C. L. da Costa, L. V. Ferreira, and P. Meir (2014), Predicting the response of the Amazon rainforest to persistent drought conditions under current and future climates: a major challenge for global land surface models, *Geoscientific Model Development*, 7(6), 2933–2950, doi:10.5194/gmd-7-2933-2014.
- Kattge, J., S. DÄNÄz, S. Lavorel, I. C. Prentice, P. Leadley, G. BÄÜNisch, E. Garnier, M. Westoby, P. B. Reich, I. J. Wright, J. H. C. Cornelissen, C. Violle, S. P. Harrison, P. M. Van Bodegom, M. ReichSTEIN, B. J. Enquist, N. A. Soudzilovskaia, D. D. Ackerly, M. Anand, O. Atkin, M. Bahn, T. R. Baker, D. Baldocchi, R. Bekker, C. C. Blanco, B. Blonder, W. J. Bond, R. Bradstock, D. E. Bunker, F. Casanoves, J. Cavender-Bares, J. Q. Chambers, F. S. Chapin Iii, J. Chave, D. Coomes, W. K. Cornwell, J. M. Craine, B. H. Dobrin, L. Duarte, W. Durka, J. Elser, G. Esser, M. Estiarte, W. F. Fagan, J. Fang, F. FernÄÄNdez-MÄÄNdez, A. Fidelis, B. Finegan, O. Flores, H. Ford, D. Frank, G. T. Freschet, N. M. Fyllas, R. V. Gallagher, W. A. Green, A. G. Gutierrez, T. Hickler, S. I. Higgins, J. G. Hodgson, A. Jalili, S. Jansen, C. A. Joly, A. J. Kerkhoff, D. Kirkup, K. Kitajima, M. Kleyer, S. Klotz, J. M. H. Knops, K. Kramer, I. KÄIJHn, H. Kurokawa, D. Laughlin, T. D. Lee, M. Leishman, F. Lens, T. Lenz, S. L. Lewis, J. Lloyd, J. LlusiÄÄ, F. Louault, S. Ma, M. D. MaHECHA, P. MaNNING, T. MaSSAD, B. E. Medlyn, J. Messier, A. T. Moles, S. C. MÄIJLler, K. Nadrowski, S. Naeem, Ä. Ninemets, S. NÄÜllerT, A. NÄIJSke, R. Ogaya, J. Oleksyn, V. G. Onipchenko, Y. Onoda, J. OrdoÄSEz, G. Overbeck, W. A. Ozinga, S. PatiÄSO, S. Paula, J. G. Pausas, J. PeÄSUelas, O. L. Phillips, V. Pillar, H. Poorter, L. Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B. Reu, L. Sack, B. Salgado-Negret, J. Sardans, S. Shiodera, B. Shipley, A. Siefert, E. Sosinski, J.-F. Soussana, E. Swaine, N. Swenson, K. Thompson, P. Thornton, M. Waldram, E. Weiher, M. White, S. White, S. J. Wright, B. Yguel, S. Zahle, A. E. Zanne, and C. Wirth (2011), Try ÄÄ a global database of plant traits, *Global Change Biology*, 17(9), 2905–2935, doi:10.1111/j.1365-2486.2011.02451.x.
- Klein, T., and S. Niu (2014), The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours, *Functional Ecology*, 28(6), 1313–1320, doi:10.1111/1365-2435.12289.
- Konings, A. G., and P. Gentine (2017a), Global variations in ecosystem-scale isohydricity, *Global Change Biology*, 23(2), 891–905, doi:10.1111/gcb.13389.
- Konings, A. G., M. Piles, K. RÄützer, K. A. McColl, S. K. Chan, and D. Entekhabi (2016), Vegetation optical depth and scattering albedo retrieval using time series of dual-polarized l-band radiometer observations, *Remote Sensing of Environment*, 172, 178 – 189, doi: <https://doi.org/10.1016/j.rse.2015.11.009>.
- Konings, A. G., A. P. Williams, and P. Gentine (2017b), Sensitivity of grassland productivity to aridity controlled by stomatal and xylem regulation, *Nature Geoscience*, 10(4), 284–288, doi:10.1038/ngeo2903.
- Lee, J.-E., R. S. Oliveira, T. E. Dawson, and I. Fung (2005), Root functioning modifies seasonal climate, *Proceedings of the National Academy of Sciences of the United States of America*, 102(49), 17,576–17,581, doi:10.1073/pnas.0508785102.
- Lin, C., P. Gentine, Y. Huang, K. Guan, H. Kimm, and S. Zhou (2018), Diel ecosystem conductance response to vapor pressure deficit is suboptimal and independent of soil moisture, *Agricultural and Forest Meteorology*, 250-251, 24 – 34, doi: <https://doi.org/10.1016/j.agrformet.2017.12.078>.
- Mackay, D. S., D. E. Roberts, B. E. Ewers, J. S. Sperry, N. G. McDowell, and W. T. Pockman (2015), Interdependence of chronic hydraulic dysfunction and canopy processes can improve integrated models of tree response to drought, *Water Resources Research*, 51(8),

- 6156–6176, doi:10.1002/2015WR017244.
- Manzoni, S., G. Vico, G. Katul, P. A. Fay, W. Polley, S. Palmroth, and A. Porporato (2011), Optimizing stomatal conductance for maximum carbon gain under water stress: a meta-analysis across plant functional types and climates, *Functional Ecology*, 25(3), 456–467, doi:10.1111/j.1365-2435.2010.01822.x.
- Manzoni, S., G. Vico, S. Palmroth, A. Porporato, and G. Katul (2013a), Optimization of stomatal conductance for maximum carbon gain under dynamic soil moisture, *Advances in Water Resources*, 62, 90 – 105, doi:https://doi.org/10.1016/j.advwatres.2013.09.020.
- Manzoni, S., G. Vico, G. Katul, S. Palmroth, R. B. Jackson, and A. Porporato (2013b), Hydraulic limits on maximum plant transpiration and the emergence of the safety-efficiency trade-off, *New Phytologist*, 198(1), 169–178, doi:10.1111/nph.12126.
- McDowell, N., A. C. D., A. Kristina, B. Paulo, B. Roel, C. Jeff, C. Brad, D. Stuart, D. Chris, D. Alvaro, E. Fernando, F. Rosie, F. C. G., G. David, G. Devin, G. Charlotte, H. Henrik, H. Jennifer, J. D. J., K. A. Rahman, K. Michael, K. Charlie, K. Lara, K. Tomo'omi, M. Yadvinder, M. S. M., M. Maurizio, M. Patrick, M. Paul, M. H. C., P. O. L., P. Thomas, S. C. A., S. John, W. Jeff, X. Chonggang, and X. Xiangtao (2018), Drivers and mechanisms of tree mortality in moist tropical forests, *New Phytologist*, 0(0), doi: 10.1111/nph.15027.
- McDowell, N. G., and C. D. Allen (2015), Darcy's law predicts widespread forest mortality under climate warming, *Nature Climate Change*, 5(7), 669–672.
- McDowell, N. G., R. A. Fisher, C. Xu, J. C. Domec, T. H. Åltt, D. S. Mackay, J. S. Sperry, A. Boutz, L. Dickman, N. Gehres, J. M. Limousin, A. Macalady, J. Martínez-Vilalta, M. Mencuccini, J. A. Plaut, J. Ogñe, R. E. Pangle, D. P. Rasse, M. G. Ryan, S. Sevanto, R. H. Waring, A. P. Williams, E. A. Yezpe, and W. T. Pockman (2013), Evaluating theories of drought-induced vegetation mortality using a multimodel experiment framework, *New Phytologist*, 200(2), 304–321, doi:10.1111/nph.12465.
- McDowell, N. G., A. P. Williams, C. Xu, W. T. Pockman, L. T. Dickman, S. Sevanto, R. Pangle, J. Limousin, J. Plaut, D. S. Mackay, J. Ogee, J. C. Domec, C. D. Allen, R. A. Fisher, X. Jiang, J. D. Muss, D. D. Breshears, S. A. Rauscher, and C. Koven (2016), Multi-scale predictions of massive conifer mortality due to chronic temperature rise, *Nature Climate Change*, 6, 295–300, doi:10.1038/nclimate2873.
- Medlyn, B. E., R. A. Duursma, D. Eamus, D. S. Ellsworth, I. C. Prentice, C. V. M. Barton, K. Y. Crous, P. De Angelis, M. Freeman, and L. Wingate (2011), Reconciling the optimal and empirical approaches to modelling stomatal conductance, *Global Change Biology*, 17(6), 2134–2144, doi:10.1111/j.1365-2486.2010.02375.x.
- Meinzer, F. C., S. A. James, and G. Goldstein (2004), Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees, *Tree Physiology*, 24(8), 901–909, doi:10.1093/treephys/24.8.901.
- Meinzer, F. C., D. M. Johnson, B. Lachenbruch, K. A. McCulloh, and D. R. Woodruff (2009), Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance, *Functional Ecology*, 23(5), 922–930, doi:10.1111/j.1365-2435.2009.01577.x.
- Momen, M., J. D. Wood, K. A. Novick, R. Pangle, W. T. Pockman, N. G. McDowell, and A. G. Konings (2017), Interacting effects of leaf water potential and biomass on vegetation optical depth, *Journal of Geophysical Research: Biogeosciences*, 122(11), 3031–3046, doi:10.1002/2017JG004145.
- Nepstad, D. C., R. de Carvalho, Claudio, E. A. Davidson, P. H. Jipp, and e. al (1994), The role of deep roots in the hydrological and carbon cycles of amazonian forests and pastures, *Nature*, 372(6507), 666.
- Novick, K. A., D. L. Ficklin, P. C. Stoy, C. A. Williams, G. Bohrer, A. Oishi, S. A. Papuga, P. D. Blanken, A. Noormets, B. N. Sulman, R. L. Scott, L. Wang, and R. P. Phillips (2016a), The increasing importance of atmospheric demand for ecosystem water and carbon fluxes, *Nature Climate Change*, 6(11), 1023–1027.

- Novick, K. A., C. F. Miniati, and J. M. Vose (2016b), Drought limitations to leaf-level gas exchange: results from a model linking stomatal optimization and cohesion-tension theory, *Plant, Cell & Environment*, 39(3), 583–596, doi:10.1111/pce.12657.
- Oleson, K. W., D. M. Lawrence, G. B. Bonan, B. Drewniak, M. Huang, C. D. Koven, S. Levis, F. Li, W. J. Riley, Z. M. Subin, S. C. Swenson, P. E. Thornton, A. Bozbiyik, R. Fisher, C. L. Heald, E. Kluzek, J.-F. Lamarque, P. J. Lawrence, L. R. Leung, W. Lipscomb, S. Muszala, D. M. Ricciuto, W. Sacks, Y. Sun, J. Tang, and Z.-L. Yang (2013), Technical description of version 4.5 of the community land model (clm), NCAR Tech. Note NCAR/TN-503+STR, *National Center for Atmospheric Research, Boulder, Colorado*, 420 pp., doi:10.5065/D6RR1W7M.
- Oliveira, R. S., T. E. Dawson, S. S. O. Burgess, and D. C. Nepstad (2005), Hydraulic redistribution in three amazonian trees, *Oecologia*, 145(3), 354–363, doi:10.1007/s00442-005-0108-2.
- Powell, T. L., D. R. Galbraith, B. O. Christoffersen, A. Harper, H. M. A. Imbuzeiro, L. Rowland, S. Almeida, P. M. Brando, A. C. L. da Costa, M. H. Costa, N. M. Levine, Y. Malhi, S. R. Saleska, E. Sotta, M. Williams, P. Meir, and P. R. Moorcroft (2013), Confronting model predictions of carbon fluxes with measurements of amazon forests subjected to experimental drought, *New Phytologist*, 200(2), 350–365, doi:10.1111/nph.12390.
- Powell, T. L., W. J. K., O. A. A. R., C. A. C. Lola, S. S. R., M. Patrick, and M. P. R. (2018), Differences in xylem and leaf hydraulic traits explain differences in drought tolerance among mature amazon rainforest trees, *Global Change Biology*, 23(10), 4280–4293, doi:10.1111/gcb.13731.
- Restaino, C. M., D. L. Peterson, and J. Littell (2016), Increased water deficit decreases douglas fir growth throughout western US forests, *Proceedings of the National Academy of Sciences*, 113(34), 9557–9562, doi:10.1073/pnas.1602384113.
- Restrepo-Coupe, N., N. M. Levine, B. O. Christoffersen, L. P. Albert, J. Wu, M. H. Costa, D. Galbraith, H. Imbuzeiro, G. Martins, A. C. da Araujo, Y. S. Malhi, X. Zeng, P. Moorcroft, and S. R. Saleska (2017), Do dynamic global vegetation models capture the seasonality of carbon fluxes in the amazon basin? A data-model intercomparison, *Global Change Biology*, 23(1), 191–208, doi:10.1111/gcb.13442.
- Sack, L., P. J. Melcher, M. A. Zwieniecki, and N. M. Holbrook (2002), The hydraulic conductance of the angiosperm leaf lamina: a comparison of three measurement methods, *Journal of Experimental Botany*, 53(378), 2177–2184.
- Scholz, F. G., N. G. Phillips, S. J. Bucci, F. C. Meinzer, and G. Goldstein (2011), Hydraulic capacitance: Biophysics and functional significance of internal water sources, in Meinzer, F.C., Lachenbruch, B., Dawson, T. E. (eds) *Size- and Age-Related Changes in Tree Structure and Function*, pp. 341–361, Springer, Dordrecht.
- Seager, R., A. Hooks, A. P. Williams, B. Cook, J. Nakamura, and N. Henderson (2015), Climatology, variability, and trends in the u.s. vapor pressure deficit, an important fire-related meteorological quantity, *Journal of Applied Meteorology and Climatology*, 54(6), 1121–1141, doi:10.1175/JAMC-D-14-0321.1.
- Sellers, P. J., D. A. Randall, G. J. Collatz, J. A. Berry, C. B. Field, D. A. Dazlich, C. Zhang, G. D. Collelo, and L. Bounoua (1996a), a revised land surface parameterization (sib2) for atmospheric gcms. part i: Model formulation, *Journal of Climate*, 9(4), 676–705, doi:10.1175/1520-0442(1996)009<0676:ARLSPF>2.0.CO;2.
- Sellers, P. J., C. J. Tucker, G. J. Collatz, S. O. Los, C. O. Justice, D. A. Dazlich, and D. A. Randall (1996b), A revised land surface parameterization (sib2) for atmospheric gcms. part ii: The generation of global fields of terrestrial biophysical parameters from satellite data, *Journal of Climate*, 9(4), 706–737, doi:10.1175/1520-0442(1996)009<0706:ARLSPF>2.0.CO;2.
- Sheffield, J., E. F. Wood, and M. L. Roderick (2012), Little change in global drought over the past 60 years, *Nature*, 491(7424), 435–8.
- Simonin, K. A., E. Burns, B. Choat, M. M. Barbour, T. E. Dawson, and P. J. Franks (2015), Increasing leaf hydraulic conductance with transpiration rate minimizes the water potential

- drawdown from stem to leaf, *Journal of Experimental Botany*, 66(5), 1303–1315, doi:10.1093/jxb/eru481.
- Siqueira, M., G. Katul, and A. Porporato (2008), Onset of water stress, hysteresis in plant conductance, and hydraulic lift: Scaling soil water dynamics from millimeters to meters, *Water Resources Research*, 44(1), W01432, doi:10.1029/2007WR006094.
- Sperry, J. S., and D. M. Love (2015), What plant hydraulics can tell us about responses to climate-change droughts, *New Phytologist*, 207(1), 14–27, doi:10.1111/nph.13354.
- Sperry, J. S., F. R. Adler, G. S. Campbell, and J. P. Comstock (1998), Limitation of plant water use by rhizosphere and xylem conductance: results from a model, *Plant Cell Environment*, 21(4), 347–359, doi:10.1046/j.1365-3040.1998.00287.x.
- Sperry, J. S., U. G. Hacke, R. Oren, and J. P. Comstock (2002), Water deficits and hydraulic limits to leaf water supply, *Plant, Cell & Environment*, 25(2), 251–263, doi:10.1046/j.0016-8025.2001.00799.x.
- Sperry, J. S., M. D. Venturas, W. R. L. Anderegg, M. Mencuccini, D. S. Mackay, Y. Wang, and D. M. Love (2017), Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost, *Plant, Cell & Environment*, 40(6), 816–830, doi:10.1111/pce.12852, pCE-16-0541.R1.
- Thornton, P. E., and N. E. Zimmermann (2007), An improved canopy integration scheme for a land surface model with prognostic canopy structure, *Journal of Climate*, 20(15), 3902–3923, doi:10.1175/JCLI4222.1.
- Tyree, M. T., and J. S. Sperry (1988), Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress?: Answers from a model, *Plant Physiology*, 88(3), 574–580.
- Tyree, M. T., and J. S. Sperry (1989), Vulnerability of xylem to cavitation and embolism, *Annual Review of Plant Physiology and Plant Molecular Biology*, 40(1), 19–36, doi:10.1146/annurev.pp.40.060189.000315.
- Ukkola, A. M., M. G. D. Kauwe, A. J. Pitman, M. J. Best, G. Abramowitz, V. Haverd, M. Decker, and N. Houghton (2016), Land surface models systematically overestimate the intensity, duration and magnitude of seasonal-scale evaporative droughts, *Environmental Research Letters*, 11(10), 104012.
- Verhoef, A., and G. Egea (2014), Modeling plant transpiration under limited soil water: Comparison of different plant and soil hydraulic parameterizations and preliminary implications for their use in land surface models, *Agricultural and Forest Meteorology*, 191, 22–32, doi:https://doi.org/10.1016/j.agrformet.2014.02.009.
- Williams, A. P., C. D. Allen, A. K. Macalady, D. Griffin, C. A. Woodhouse, D. M. Meko, T. W. Swetnam, S. A. Rauscher, R. Seager, H. Grissino-Mayer, J. S. Dean, E. R. Cook, C. Gangodagamage, M. Cai, and N. G. McDowell (2013), Temperature as a potent driver of regional forest drought stress and tree mortality, *Nature Climate Change*, 3(3), 292–297.
- Williams, M., E. B. Rastetter, D. N. Fernandes, M. L. Goulden, S. C. Wofsy, G. R. Shaver, J. M. Melillo, J. W. Munger, S.-M. Fan, and K. J. Nadelhoffer (1996), Modelling the soil-plant-atmosphere continuum in a quercus stand at harvard forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties, *Plant, Cell & Environment*, 19(8), 911–927, doi:10.1111/j.1365-3040.1996.tb00456.x.
- Williams, M., B. E. Law, P. M. Anthoni, and M. H. Unsworth (2001), Use of a simulation model and ecosystem flux data to examine carbon–water interactions in ponderosa pine., *Tree Physiology*, 21(5), 287 – 298.
- Xu, X., D. Medvigy, J. S. Powers, J. M. Becknell, and K. Guan (2016), Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests, *New Phytologist*, 212(1), 80–95, doi:10.1111/nph.14009, 2015-20772.
- Zhou, S., R. A. Duursma, B. E. Medlyn, J. W. Kelly, and I. C. Prentice (2013), How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress, *Agricultural and Forest Meteorology*, 182-183, 204 – 214, doi:https://doi.org/10.1016/j.agrformet.2013.05.009.

1473 Zhou, S., B. Medlyn, S. Sabaté, D. Sperlich, I. C. Prentice, and D. Whitehead (2014), Short-  
1474 term water stress impacts on stomatal, mesophyll and biochemical limitations to photosyn-  
1475 thesis differ consistently among tree species from contrasting climates, *Tree Physiology*,  
1476 34(10), 1035, doi:10.1093/treephys/tpu072.