

General comment to the reviewer: Thank you for taking the time to thoroughly read our manuscript and in particular, for highlighting the key parts of the paper which were unclear. We believe that our revisions make a substantial improvement to the accessibility of the description of the model and why we pursued our particular approach to a broad audience. Below, your original comments are highlighted in red and our responses are in black. When text is copied directly from the revised paper the words are italicized.

This paper presents a plant hydraulic model and the parameterization of this model with plant traits of tropical forest trees. The study is interesting and in the scope of the journal *Geoscientific Model Development*. The hydraulic model itself is based on the model proposed by Sperry et al. (1998). But the parameterization with plant traits is comprehensive and valuable for model development, especially for modeling tropical forests. The equations in Supplement S1 have well explained the formulations of the model. And the figures and the equations in Table 2 are presenting the results well.

Thank you for recognizing the value of our research.

I have to say that I had a hard time reading this paper. I went through this paper many time in the past weeks and still didn't well get it. Fortunately, the equations in Supplemental material and Table 2 are clear and the figures of results are readable. I can see it is a good work. But the writing of this paper should be substantially improved in its revised version.

We made substantial changes in four main places of the manuscript where the model is either introduced or described: The introduction (1.), the model overview (2.1.1), the tissue water relations (2.1.2), and scaling conductance with tree size (2.1.4). Several other minor modifications to text were also made. We describe these changes in detail in our response to your "Minor suggestions" #1, #2, #3 and #6 below.

Another concern is the interactions between the hydraulics model and the host model TFS. The authors only show that the hydraulics model makes the hourly predictions of water dynamics better (e.g., transpiration, water potential, etc.) at given forest structure in their results. But, how the hydraulics model affects the long-term predictions of TFS (decades to a century)? I ask this question because a plant hydraulics model may change the behavior of trees in competition and therefore change the long-term predictions of forest dynamics. I want to know to what extent it changes the host model (i.e., TFS).

We agree that the interactions between plant hydraulic traits and longer term demographic dynamics is a scientifically intriguing and important topic and is one we intend to pursue, but in future work. The current version of TFS we are using is not as of yet dynamic – mortality and recruitment processes are not yet fully developed. The model in its current form requires site-specific initialization and is intended to explore (and be validated by) various short-term demographically-structured outputs, such as productivity and (in the case of the hydraulics mode) water status of individual trees.

The validation exercises conducted by Fyllas et al. (2014) and this paper give us confidence to proceed with the analysis you suggest. We highlight how the novel model capability described here fits within the broader scope of interactions between plant hydraulic traits and forest trait composition and dynamics in two new sentences at the end of the Discussion overview paragraph (page 26 line 27 – page 27 line 2):

In sum, TFS v.1-Hydro represents a key and advanced model capability to represent differential performance of individual trees based on hydraulic traits, size and light environments (Figs 9-10). Future work coupling the present scheme with community dynamics (mortality, growth and recruitment) has the potential to predict shifts in community trait distributions under changing moisture regimes, as has been observed or implied in studies of tropical species distributions and forest community dynamics (Engelbrecht et al., 2007; Fauset et al., 2012).

Minor suggestions:

1. The section of “introduction” : I didn’t get it why it is necessary to build this model and why this way works here from this section. I hope the authors can write a better introduction to make it easier to understand in a revised version.

We have expanded the section outlining the various approaches to doing plant hydraulics (page 3 line 27 – page 5 line 8), in order to highlight why we elaborated (what we have now termed) the “continuous porous media” approach:

While a range of approaches exist for modeling plant hydraulics at fine scales (i.e., individual trees), all involve an extension of Darcy’s law (Darcy, 1856) from the soil domain to include plants as well. Darcy’s law states that water flux anywhere in the soil-plant continuum is proportional to the product of soil or plant hydraulic conductivity and a gradient in water potential. In order for these models to capture drought response, hydraulic conductivity within the soil-plant continuum must dynamically respond to changes in moisture. Three main approaches are distinguished in terms of how they represent the impact of declines in water potential on tissue water content and xylem hydraulic conductivity. A first class of models is the simplest and simulates moisture sensitivity of soil-root conductance but not xylem hydraulic conductance (Jarvis et al., 1981; Williams et al., 1996; Ogée et al., 2003; Alton et al., 2009; Bonan et al., 2014). This approach has proven useful for modeling the effects experimental drought in tropical forests (Williams et al., 1998; Fisher et al., 2006; Fisher et al., 2007), but it remains unclear whether this approach misattributes drought effects occurring within trees to the soil; therefore a second class of models implements variable xylem conductivity with xylem water potential (Williams et al., 2001; Hickler et al., 2006; Domec et al., 2012; Duursma and Medlyn, 2012; Xu et al., 2016). To simplify computational load, these two approaches do not explicitly track dynamic changes in the volume of plant water storage. Instead, a constant ratio of change in stored water per unit change in water potential, or stem hydraulic capacitance, is assumed, which may overestimate the buffering capacity of tree stored water under extreme drought conditions when small relative declines in stored water induce very large declines in water potential. An additional consequence of the design of these models is the inability to represent the bidirectional flow of water at the root-soil interface. Reverse flow of water from roots into soil is an important process in root hydraulic distribution (Oliveira et al., 2005), and may also mediate time to desiccation under drought (North and Nobel, 1997).

A convenient way to address these issues is in a third class of models (hereafter the “continuous porous media approach”), which simply extend the modeled mass balance of water from the soil domain into the plant by relating simulated changes in water content to water potential (and vice versa) everywhere within the plant-soil continuum (Edwards et al., 1986; Arbogast et al., 1993; Sperry et al., 1998; Kumagai, 2001; Bohrer et al., 2005; Mackay et al., 2015; Mirfenderesgi et al., 2016). While more computationally complex, the continuous porous media approach offers two main advantages in addition to addressing the issue of plant water storage and bidirectional root flow. First, the coupled plant-soil system is represented by a single mass balance equation, such that root water uptake or loss simply emerges from the solution of this equation, and needs not be ascribed post-hoc as is the case in the first two approaches. Second, this approach relies on an explicit description of the relationship between water content and water potential in plant xylem (the “pressure-volume”, or PV curve), analogous to the water retention curves used in soil physics. As we will show, there is a wealth of information on PV hydraulic traits for leaves, and to a lesser degree, stems in tropical forests. Implementing PV curves in the model greatly increases the scope of data with which the model can be parameterized. In this paper, we develop a continuous porous media approach intended for application at specific sites in the tropics to explore dynamics of water fluxes from hourly to seasonal timescales and at spatial scales ranging from individual trees to the stand-level scale. This intermediate-scale approach is a model testbed meant to inform implementations of plant hydraulics in coarse-scale forest ecosystem models.

We have also better highlighted (page 5, line 28 – page 6, line 8) why plant hydraulics is important from a long-term demographic and trait-filtering perspective (which will give rise to the kinds of long-term investigations you highlight above):

The implication for ecosystem models is that under-representation of diversity in functional traits and tree size in tropical forests is undermining efforts to make accurate projections of tropical forest response to climate. Model parameterization of hydraulic trait diversity should thus provide much-needed model capability to represent a diversity of responses to changes in moisture availability, laying the groundwork for representing trait-mediated differences in survival and subsequent shifts in forest trait composition. Shifts in trait composition are already occurring in some tropical forests (e.g., Enquist and Enquist, 2011; van der Sande et al., 2016), and such shifts (or the diversity of traits alone) have been shown to buffer ecosystems in the face of environmental change, and in some cases, are the difference between predicted complete loss of forest and forest persistence (Fauset et al., 2012; Levine et al., 2016; Sakschewski et al., 2016).

2. In page 4, lines 36 “Other models treat the plant continuum as a porous medium with constitutive equations defining water retention properties (the relationship between water potential and water content) and xylem PLC, using Darcy’s law to incorporate fluxes within the Richards’ mass balance equation”. I think this sentence is important because it describes what other models do. But please make this sentence clear.

This description has been entirely re-worked and is given in the response to your comment immediately above

3. Pages 45, from line 10 in page 4 to line 30 in page 5: These two big paragraphs have a lot of facts and arguments. But they are too messy. I have read through them many times, trying to figure out the messages that the authors want to deliver. But, I still do not get them.

We have substantially restructured these paragraphs to highlight our important messages, by deleting some content and adding some clarifying sentences that link this section to the previous section summarizing modeling approaches, as follows (page 5, lines 9 – 15):

Model parameterization leads us to the challenge of how to represent variation in plant hydraulic traits governing moisture sensitivity and water transport capacity. It has long been recognized that the functional trait diversity of tropical forests mirrors their large species diversity (Corner, 1949; Hallé et al., 1978; Leigh Jr, 1999), and diversity in plant hydraulic traits such as the water potential at turgor loss (π_{tlp}) and at 50% loss of conductivity (P_{50}), xylem-specific hydraulic conductivity ($k_{s,max}$) and the leaf-to-sapwood area ratio ($A_l:A_s$) is no exception (Borchert, 1994; Tobin et al., 1999; Lopez et al., 2005; Meinzer et al., 2008a; Zhu et al., 2013).

We then proceed with our original summary (which has been reworded in some places) of various lines of evidence indicating how plant hydraulic traits can ultimately affect the distribution of species and their various hydraulic strategies across gradients in water availability (page 5, line 15 – page 6, line 8).

4. Page 7, lines 910 “: : : the model developed by J.S. Sperry and described in Sperry et al. (1998)” can be shortened as “: : : the model developed by Sperry et al. (1998)”.

Done.

5. Page 7, line 21 “we modified S98 in three important ways : : :”. I prefer to say “we modified S98 in three ways : : :” by crossing out “important”. I understand that these modifications are important. But here it’s a description of the model and you don’t have to evaluate your works here.

We have eliminated value statements about our modeling approach from the Methods section.

6. Page 8 lines 112: This paragraph should be a summary of the model, not just what have been described in Supplement S1. The authors should expect the readers to get a picture of the model by their descriptions without reading S1.

We have substantially re-worked the model overview section (page 8, line 5 – page 9, line 9) to summarize the model for readers so that they do not have to read S1 to understand its structure. We maintained references to the Supplement S1, however, so that readers can refer to it for further details not included in the main text:

The fast-timescale dynamics of the hydraulics model are governed by three sets of constitutive relationships: 1) the relationship between water potential and water content, 2) the relationship between hydraulic conductivity and water potential, and 3) the relationship between a stomatal water stress multiplier and leaf water potential. The first two relations are applied to every compartment within the plant-soil continuum and have specific equations for plant and soil porous media types. The soil constitutive equations for the first two relations are given by, respectively, the van Genuchten (1980) and Mualem (1976) formulations. We chose these particular equations for the soil water characteristic and unsaturated hydraulic conductivity because extensive work has parameterized these formulations on tropical soils, which have been noted to have distinct hydraulic properties when compared to temperate soils of similar texture (Tomasella and Hodnett, 2002). These equations are given in the Supplement S1 Sections 3.1.2 and 3.2.2. The plant constitutive equations for the first two relations are formulated and described in Sections 2.1.2 and 2.1.3 below. The third relation for stomatal response to moisture stress is described in Section 2.1.5. All parameters of the constitutive relations for plant tissue are biologically interpretable and measureable plant hydraulic traits.

Several linkages are made between tree allometry and hydraulic properties (see Supplement S1 Section 4). Leaf, stem, transporting root, and absorbing root water storage compartment volumes derive respectively from the TFS-predicted leaf, stem, coarse root, and fine root biomasses using characteristic tissue densities. The heights of these components derive from tree height and rooting depth. The characteristic soil volume over which root uptake occurs is given by half the distance between absorbing roots, which decreases as total community root length (summed across all trees) increases. Total hydraulic conductance between adjacent plant water storage compartments is scaled from xylem hydraulic conductivity using first principles and plant allometric theory (Section 2.1.4). The model code only initializes these allometrically-dependent hydraulic properties; it does not (yet) implement functions to update them as trees grow. Neglecting the effects of growth has negligible effects on the results presented in this paper but will be necessary for application of the model at timescales longer than one year.

The numerical solution (see Supplement S1 Section 5) operates at every timestep and updates water contents and potentials throughout the plant-soil continuum (including root uptake or loss) due to transpiration. It uses a first-order Taylor series expansion about the water content term to linearize the Richards mass balance equation describing the 1-dimensional continuous array of plant and soil compartments. This results in a tridiagonal matrix that is solvable without iteration. Following the approach of Siqueira et al. (2008), infiltration and drainage are treated separately from the plant-soil fluxes due to transpiration (Supplement S1 Section 6).

7. Page 8, lines 2223: It took me a while to think what the authors want to tell in this sentence. If the authors just want to talk about “capillary water”, I prefer a sentence like “sapwood also stores capillary water in its void spaces and embolized conduits”. Then, I don’t have to think about “tension theory”.

This sentence has been modified as suggested.

8. Page 8 lines 2330: These arguments are not necessary because this section is to describe the model. And, the sentences in lines 1423 can be reorganized so that it’s easier for readers to understand Eqn 1.

We have eliminated value statements about our modeling approach from the Methods section. We deleted unnecessary details from the paragraph leading up to Eqn 1 and

added a sentence at the end to make it easier to understand Eqn 1. This paragraph now reads as:

We used pressure-volume (PV) theory (Bartlett et al., 2012; Tyree and Hammel, 1972; Tyree and Yang, 1990) to describe the constitutive relation between total water potential (ψ_{tot} , MPa) and relative water content (RWC, $\text{g H}_2\text{O g}^{-1} \text{H}_2\text{O}$ at saturation) in the plant compartments (Eqn 1). ψ_{tot} is the sum of two components: solute potential ψ_{sol} (MPa) which is negative due to the presence of solutes in living cells, and pressure potential ψ_p (MPa) which is ≥ 0 due to cell wall turgor (but see Ding et al., 2014). PV theory is usually applied to leaves, but can also apply to sapwood (Chapotin et al., 2006; Meinzer et al., 2008b; Scholz et al., 2007); thus we apply it here to all plant tissue. Sapwood also stores capillary water (Tyree and Yang 1990) in its void spaces and embolized conduits. Consequently, this relation is described by three successive dehydration phases representing, respectively, capillary water (sapwood only), elastic cell drainage (positive turgor), and continued drainage after cells have lost turgor: [equation 1]

9. Page 9, line 6: “RWC” is not explained.

It is now explained.

10. Page 10, line 13 “(-)”: Does it mean ax is negative? If yes, I prefer to use “-ax” in the equation.

“(-)” was changed to “(unitless)”

11. Page 11, lines 213: This paragraph is supposed to describe some “first principles” of the size effect of trees on plant hydraulics according to the second paragraph, but where are they? I saw “two main mechanisms”. The second one describes two possibilities. Which one should be the “first principle” in the model?

The Section 2.1.5 including the paragraph to which you refer was substantially re-worked (page 11, line 19 – page 12, line 22) to make clear our scaling approach to the reader:

Tree size exhibits a first-order control over much variation in whole-plant hydraulic conductance (Sperry et al., 2008) since hydraulic path length increases with tree height (H) (Mencuccini, 2002). For this reason, whole plant conductance is not a constant parameter in our model. Rather, first principles dictate that, to a first approximation, whole-tree maximum aboveground conductance ($K_{max,tree,ag}$; $\text{kg s}^{-1} \text{MPa}^{-1}$) may be derived as a function of xylem conductivity ($k_{s,max,x}$; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$), sapwood area (A_s ; m^2), and H (m) as

$$K_{max,tree,ag} = \frac{k_{s,max,x} A_s}{H} \quad (5)$$

This relation predicts the negative effects of H (increasing H means decreasing $K_{max,tree,ag}$). Whole-tree conductance per unit leaf area ($K_{l,max,tree,ag}$) will determine water status at the level of individual leaves, and thus hydraulic constraints on leaf-level gas exchange. Dividing through by leaf area (A_l ; m^2) gives

$$K_{l,max,tree,ag} = \frac{k_{s,max,x}A_s}{HA_l} \quad (6)$$

In this relation, the leaf:sapwood area ratio ($A_l:A_s$) emerges as a key plant trait controlling $K_{l,max,tree,ag}$. If $A_l:A_s$ decreases with tree height, as has been documented in many tree species (McDowell et al., 2002, but see Calvo-Alvarado et al., 2008), the negative effects of height can be partially overcome. In addition, the near-universal tendency for xylem conduits to increase in diameter within trees from stem tips to trunk base (referred to as xylem taper in the opposite direction) (Meinzer et al., 2010; Mencuccini et al., 2007; Olson et al., 2014; Olson and Rosell, 2013; Petit and Anfodillo, 2011) also mitigates the negative effects of height according to the Hagen-Poiseuille law. Neglecting the effects of xylem taper may thus overestimate the negative hydraulic effects of increasing path length in size-structured forests. Metabolic scaling theory (MST) makes baseline predictions about the optimal degree of xylem conduit taper in trees subject to the constraint of hydraulic safety (which decreases as conduits get larger) and has been validated against observations of conduit diameter across trees of different heights (Savage et al., 2010; West et al., 1999). We therefore use MST to include the effect of xylem taper on $K_{l,max,tree,ag}$ by modifying Equation 6 to include a xylem taper term ($\chi_{tap:notap,ag}$; unitless) representing the ratio of whole-plant conductance with taper to that without:

$$K_{l,max,tree,ag} = \frac{k_{s,max,petiole}A_s}{HA_l} \chi_{tap:notap,ag} \quad (7)$$

where $k_{s,max,petiole}$ ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) is used to reference $K_{l,max,tree,ag}$ to MST predictions. $\chi_{tap:notap,ag}$ is in the range of 23-50 for trees of heights 10-30 m; thus the benefit of xylem taper for increasing total plant conductance itself increases with tree height. $\chi_{tap:notap}$ is assumed constant across individuals in this study, but parameterizing variation in $A_l:A_s$ across species is an outcome of this study. The full details of this approach in addition to the treatment of the belowground component of tree conductance ($K_{max,tree,bg}$) are outlined in Section 2 of the Technical Description (Supplement S1).

12. Page 11, line 10: “because of the Hagen-Poiseuille law”. It’s a phenomenon of the Hagen-Poiseuille law, not because of it.

This was changed to “according to”

13. Page 12, lines 2023: I think the sentence “FMCgs : : : is the only variable passed from the hydraulics module to the host model” is the message of this paragraph and therefore should be the first sentence.

We moved this sentence to be the first sentence.

14. Lines 2326 in Pages 12 and lines 15 in page 13: These sentences can be moved to discussion. This section is to describe the model, it’s not necessary to argue these issues here.

Done – these sentences were moved to become the third paragraph in the ‘Practical Implications’ Section 5.3 of the Discussion (page 30, lines 17 – 27).

15. Page 13, line 28: Please also cite Strigul et al. 2008 for PPA.

Done.

16. Page 16, line 15: “Idealized model experiments”. I would use “Model experiments” because any model experiments are always “idealized” somehow.

Done. Other references to “idealized model experiments” in the manuscript were also changed

17. Page 17, lines 1314 “We matched simulated trees : : :” It would be clearer if there is a table to show the settings of trees.

Great suggestion. We made a new Table 3 to this effect and now refer to it on page 18 line 5 and Figure 11 caption. This new table is reproduced below:

Table 3. Properties of simulated and observed trees given in Figure 11.

Figure 11 sub-panel	Tree ID*	Observed DBH (cm)	Simulated DBH (cm)	Simulated Canopy Layer	Simulated $A_1:A_s$ ($m^2 cm^{-2}$)	Simulated $K_{max,ag}$ ($kg s^{-1} MPa^{-1}$)
a,b	C1	15.6	15.6	2	0.41	0.062
c,d	C2	18.7	18.8**	2, 3	0.45**	0.064**
e,f	C4	43.9	43.9**	1, 2	0.74**	0.076**
g,h	C3	51.4	51.4	2	0.81	0.078

* as given in Fisher et al. (2006)

** two simulated trees were included in this size class. Value given is the average of the two trees.

18. Figures 11 and 13: explain “50% TFE” in legends.

Per the suggestion of Referee #1, we have removed the analyses related to TFE in this paper.

References

Fyllas, N. M., Gloor, E., Mercado, L. M., Sitch, S., Quesada, C. A., Domingues, T. F., Galbraith, D. R., Torre-Lezama, A., Vilanova, E., Ramírez-Angulo, H., Higuchi, N., Neill, D. A., Silveira, M., Ferreira, L., Aymard C, G. A., Malhi, Y., Phillips, O.

L., and Lloyd, J.: Analysing Amazonian forest productivity using a new individual and trait-based model (TFS v.1), *Geoscientific Model Development*, 7, 1251-1269, 2014.