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Comment on hess-2020-671

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Referee comment on "Plant Hydraulic Transport Controls Transpiration Response to Soil Water Stress" by Brandon P. Sloan et al., Hydrol. Earth Syst. Sci. Discuss., https://doi.org/10.5194/hess-2020-671-RC3, 2021

The manuscript by Sloan and coworkers presents a hierarchy of soil-plant-atmosphere models describing environmental and plant controls on transpiration. This hierarchy starts from a simple plant hydraulic model (minimalist PHM) that assumes a fixed soil-to-leaf hydraulic conductance and a leaf water potential dependent stomatal regulation. A more physiologically detailed model follows (complex PHM), which includes soil water potential dependent soil-to-root conductance and xylem water potential dependent plant conductance, in addition to leaf water potential regulation of stomatal conductance. The simpler ‘β model’ (empirical piecewise relation between soil moisture and transpiration rate) is found to be a limit solution of the PHMs when the soil-to-leaf conductance tends to infinity. Finally, a land surface model (LSM) is proposed based on CLM version 5, and various transpiration regulation schemes are implemented to compare them in a realistic setting. The simple β model is shown to perform well after it is modified to include atmospheric water demand.

This topic is suitable for HESS and is timely given the ongoing discussions on how to develop and implement plant hydraulic modules in land surface and ecohydrological models. The manuscript is also framed in a nice pedagogic way, from simple to complex models (a schematic roadmap of the various models used could also be useful). Overall the approach is sound, but I have some technical concerns and comments, and suggestions to improve clarity and provide an easier roadmap for the reader. Minor editorial comments are listed at the end.

Main comments

- Units and unit conversions: water flows are expressed in terms of W/m^2, which is fine, though not immediately intuitive for hydrologists. However, some choices of units are unusual (in most cases the choice will have no consequences on the model results). For example, expressing vapor pressure deficit in MPa (L80) is not consistent with usual units of kPa or mol/mol. The driving force of evaporation is typically expressed as amolar concentration difference (as also explained in L256 of the Supplement), and using a water potential difference would require some transformations because the water potential of water vapor is not a linear function of molar concentrations. Later, vapor pressure deficit is expressed in Pa (L113); I suggest making units consistent throughout. Stomatal conductance to water vapor is expressed in mol_H2O/m^2/s, but conductances are typically expressed in units referring to the carrier medium, while driving forces have the units of the scalar being transported. Here stomatal conductance should have units of mol_air/m^2/s and vapor pressure deficit mol_H2O/mol_air (=Pa/Pa). A dimensional analysis of the second term of Eq. (9) gives the same result. Similar issues arise in Eq. (13), where I could not recover the desired units for T_d.

  BPS: Thank you for this comment. The confusion is due to typos on my part. The stomatal conductance units should be mol air/m^2/s as you mention. Furthermore, the dimensional analysis in Eq. 13 fails because ρ_m should have been in the denominator and not the numerator. In order to rectify these issues and to be more consistent with widely recognized units, we will make the following to the updated manuscript:

  - **Change transpiration fluxes from W/m^2 to mm/day to appeal to a wider hydrology-based audience.**
  - **Change all supply conductances (g_{sp}, g_{sx}, and g_{xl}) to mm/day/MPa in both the minimalist and complex analysis.**
  - **Update the stomatal conductance (g_s) units to mol air/m^2/s and provide vapor pressure differences in units mol H_2O/mol air. Then, we will include the conversion factor from molar flux (mol H_2O/m^2/s) to volume flux (mm/day) for clarity.**

- Model calibration (Table S3): the LSM is rather complex, with 15 free parameters. I wonder if some parameters could be prescribed to facilitate the calibration. For example, soil parameters and LAI might be constrained based on site-specific information. Some plant parameters could also be taken from the literature. The water potential at 50% loss of conductivity for Ponderosa pine ranges between -2 and -4 MPa (Domec and Pruyn, 2008; Maherali and DeLucia, 2000; Stout and Sala, 2003), very much in line with the calibrated value, and xylem conductivities are a bit lower than the calibrated parameters (see references above). Instead, the value of water potential at 50% stomatal closure is really low at almost -10 MPa. Pinus ponderosa is a rather conservative species when it comes to stomatal closure, with nearly full closure around -2 MPa (DeLucia and Heckathorn, 1989). This suggests that in the model stomatal closure essentially does not occur until the xylem is completely cavitated, which does not seem reasonable - perhaps a result of co-variation with other not well-constrained parameters?

  BPS: Thank you for pointing this out and providing these helpful resources. You are correct that this result is due to co-variation of poorly constrained parameters. Primarily, the soil water characteristic parameters (b and ψ_{sat}) determine the soil and leaf water potential ranges and, hence, the plant hydraulic parameters. As shown in Figure 3, we are dealing with a wide range of water potentials (down to -15 MPa), which results in our unrealistically low $\psi_{l,50}$.

  To remedy this parameter, we have added an additional step to the calibration process. We have selected the parameters from Table S3 that are directly related to plant hydraulics (Table RC1) and adjusted them to match the original transpiration downregulation behavior of the calibrated parameters (solid lines in Fig. RC1a). Specifically, we fixed the values $\psi_{l,50}$ and $\psi_{x,50}$ to -1 MPa and -2.6 MPa from the resources you have provided. Then, we fit a new model (red

dots in Fig. RC1) to the old calibrated model (solid lines in Fig. RC1a) by performing constrained nonlinear least squares with the remaining 7 parameters bounded by literature values.

Table RC1: The original and new calibration parameters or the LSM version with PHM downregulation scheme. We selected a subset of 8 parameters from the original 15 (Table S3) to adjust and obtain more realistic values. The bold numbers were fixed in the second calibration step, while the other values were determined through nonlinear least squares and matching the original transpiration downregulation behavior (Figure RC1).

Parameter	Description	Units	Original	New
K_{sap}	Sapwood-specific hydraulic conductivity	kg m^{-1} s^{-1} MPa^{-1}	0.47	1.4
$\psi_{x,50}$	Xylem water potential at 50% loss of conductance	MPa	-2.3	**-2.6**
a	Xylem vulnerability curve shape parameter	-	0.3	0.57
$\psi_{l,50}$	Leaf water potential at 50% loss of conductance	MPa	-9.9	**-1**
b_l	Leaf vulnerability curve shape parameter	-	3.4	5.38
b	Soil retention curve exponent	-	5.1	3.78
$\psi_{s,sat}$	Saturated soil water potential	MPa	$-9.9e^{-3}$	$-5.6e^{-3}$
$K_{s,sat}$	Saturated soil hydraulic conductivity	m d^{-1}	10	0.66

This second fitting step allowed to us to replicate the original model's transpiration downregulation behavior with parameter values more in line with literature (red dots in Fig. RC1a). This parameter adjustment had negligible impact on the overall LSM performance (Fig. RC1b) because the LSM suffers from equifinality (i.e., multiple parameter sets give the similar model output). Therefore, we avoided having to re-run the expensive grid search method (13,600 separate runs) with more realistic parameter bounds by simply nudging the parameters to more realistic values without loss of performance.

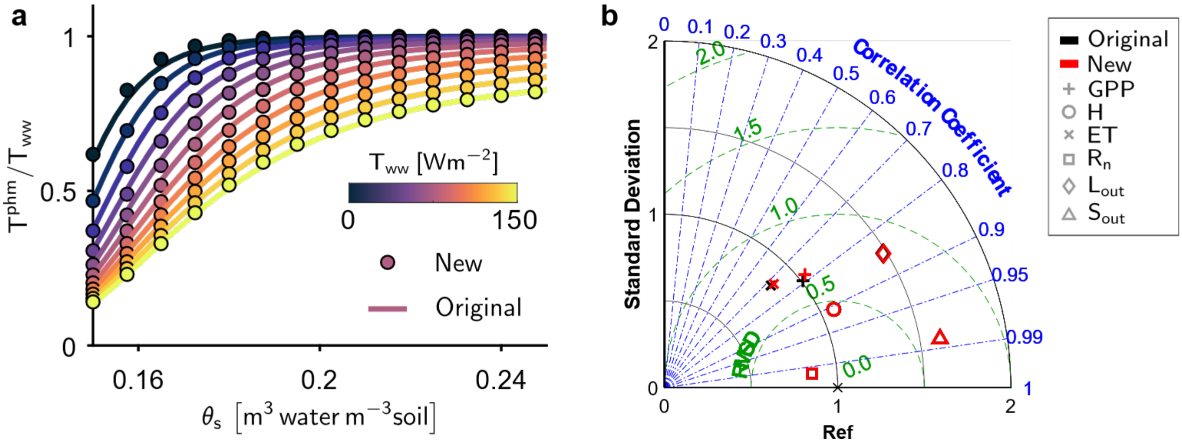

Figure 1: a) Comparison of the transpiration downregulation for the original calibrated LSM parameters (solid lines) to the newly updated parameters (filled circles) in Table RC 1. The parameters closely replicate the downregulation behavior of the original parameters while provding more realistic plant hydraulic traits compared to literature. We focus on the range of soil water content measured at the site and the range of well-watered transpiration rates calculated from the well-watered LSM (see Sect. 3.3 and Fig. 4a-b in the paper for more details on this plot). b) The Taylor diagram comparing LSM predictions for the original and new calibration parameters for evapotranspiration (ET), sensible heat flux (H), gross primary productivity (GPP), net radiation (R_n), outgoing shortwave radiation (S_{out}) and outgoing longwave radiation (L_{out}). The LSM predictions are negligibly affected by our shifting of parameter values, which is a sign of equifinality.

In the revised manuscript, we will update Figs. 3-4 with these new LSM results and detail additional calibration steps in Sect. 2.3. Furthermore, we will include Figs. RC1 and RC2 in the supplement to help explain our method.

- Definition of water transport regimes: I was a bit confused by the definitions of supply- limited, demand-limited, and transport-limited conditions. L208: supply is not really limited if the soil-to-leaf conductance is large - this condition would more demand- limited. L301: also in this case, I would think of riparian systems as not supply-limited. Perhaps the terminological issue arises because ‘supply’ in my mind refers to the whole soil-plant system, and ‘demand’ refers to the plant-atmosphere system.

BPS: Thank you for this comment. We do agree that supply-limited may be confusing. We want to convey that, as transport effects diminish (g_{sp} becomes large), soil water potential limits transpiration as it approaches leaf water potential and induces stomata closure. To avoid associating ‘supply-limited’ systems with ‘dry’ systems, we will replace the term ‘supply-limited’ with ‘soil-limited’ in the updated manuscript. We think this terminology locates the limiting entity to be in the soil (rather than in the atmosphere, due to demand), and overcomes the ambiguities around ‘demand-limitation’ (which applies to both soil- and transport-limited systems). We will also elaborate that the name is due to soil water potential being the limiting factor.

Minor comments

MAIN TEXT

A figure schematically illustrating the model hierarchy, and how the different models are compared and interfaced would be a useful roadmap for the reader.

BPS: We like this idea and plan to implement a two panel figure showing β and PHM model structure differences across the complex and minimalist versions.

L38: β functions per se only include soil moisture effects on transpiration, so they are insensitive to atmospheric dryness by construction - do you mean that the overall transpiration model is insensitive because of the multiplicative coupling of β and atmospheric demand?

BPS: Yes, we mean the latter. In line 27 we state that “β” refers to the downregulation model in this paper whereas “β function” refers to the actual function of soil moisture. We will clarify this statement in the updated manuscript to convey that it is TBMs using the β model that are insensitive to atmospheric dryness.

L52: through acclimation as well.

BPS: We will add this in the updated manuscript.

L53: also the intermediate step of upscale to plant level is not trivial, since plants are not uniform cylinders but have branching architecture with progressive and nonlinear variations in hydraulic properties along the water flow pathway.

BPS: This is a good point and will be added in the updated manuscript.

L60: for clarity I would suggest to add “water” in front of “supply-demand framework”.

BPS: We will add this in the updated manuscript.

L74: in Manzoni et al. (2014) we did not assume a fixed soil-to-leaf conductance - our approach was more similar to the complex PHM, but with some simplifications aiming to obtain analytically the soil moisture thresholds in β as a function of plant traits and soil properties.

BPS: This was my misunderstanding. In the updated manuscript, we will remove the citation and

provide justification for removing hydraulic limits in the minimalist model. As we find later in the paper, the hydraulic limits only accentuate our conclusions, as it is the presence of a finite conductance that causes the differences between PHM and β.

L123: how are least squares used in this context?

BPS: We recast the mass balance between segments as a nonlinear least squares problem where the residuals are the differences in segment flows and the decision variables are the water potentials at the segment endpoints. We will include this description in the updated manuscript.

L243: extra “the”.

BPS: Thank you, will fix in the updated manuscript.

L247 (and in the abstract L11): I am not sure I follow how variability of water demand comes into play - the results are about values of transpiration rates, not variability.

BPS: We explain this in the sentences following line 247. In our supply-demand framework, β is an upper bound to the PHM downregulation as conductance becomes infinite. Therefore, as T_{ww} increases, PHM and β diverges according to our analysis. However, in practice, β is empirical and could be fit anywhere in the range of PHM behavior depending on data or assumed parameters. For example in our LSM analysis, we fit β to mean T_{ww} conditions (Fig. 4a,b), resulting in errors when T_{ww} was higher or lower than the mean value (instead of just high). Therefore, we must clarify that transport-limited soil-plant systems that experience high ranges (or variability) of T_{ww} over time will have a wide envelope of downregulation behavior that cannot be adequately described with a single β curve.

In the updated manuscript, we will articulate this point more clearly and add light gray shading to Fig. 3b,d,f to illustrate this PHM downregulation envelope (see below Fig. RC2). Hopefully this will drive home the point that β cannot adequately capture the range of PHM behavior.

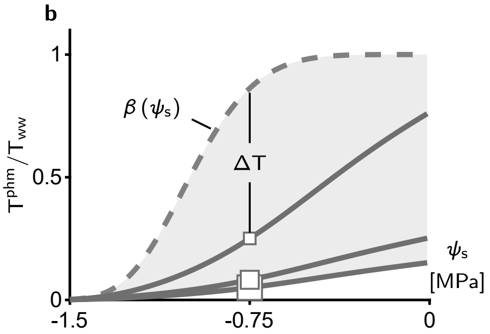

Figure 2: A look at the proposed update to Fig. 3b,d,f to help illustrate the importance of T_{ww} variability. The shaded gray region represent the variation in downregulation of the PHM with respect to T_{ww} and ψ_s. Although we show bete here as an upper bound, in practice, it is fit to data and could occupy any region in this envelope. This envelope increases with a larger range of T_{ww}, making a single β curve inadequate to cover this behavior.

L268: if the model was calibrated, where does the bias originate? Does it originate because the calibration does not minimize square differences only, but uses a more complex objective function (Eq. (S4))?

BPS: We agree that the complex objective function could contribute to the biases, although we created the function to help mitigate bias. However, we think the more likely source of bias is our grid search method. Unlike more traditional calibration methods (regularized least squares, Bayesian

optimization), the grid search does not guarantee unbiased or minimum error variance estimators. Furthermore, we are essentially performing a multi-objective optimization, so there are performance trade-offs between the fits of each flux (Fig. S6) that contribute as well to the bias.

L323: the point raised that an empirical correction of the β function works well is consistent with the results presented, but generalizing this result is difficult - if every site requires a calibration of the corrections to the β function, then it becomes simpler to use a full PHM. A comment on how results could be generalized would be useful.

BPS: We received similar comments from Reviewers 1 and 2 and will elaborate on this point in the updated manuscript. Currently, we are working on another paper validating the dynamic β form and relating its parameters to measurable plant hydraulic traits. In this paper, the dynamic β is a potential parsimonious alternative to PHMs that illustrates our main finding that coupling between atmospheric moisture demand and soil water stress is what provides PHMs superior performance. We will discuss that general implementation is future work and that dynamic β can be used to reduce computational burden but care must be taken in using the parameter relationships in this paper as they apply only to US-Me2.

SUPPLEMENT

Supplementary information: I would present first the LSM, and then results obtained using that model. Describing LSM input data and results before describing the model makes the supplement hard to read. This re-ordering of the sections would also allow referring to them in order in the main text.

BPS: We will do this in the updated manuscript.

Table S1: in the main text hydrological fluxes are expressed in W/m^2, here energy fluxes are expressed in water depth units. Reversing the units or using consistent units throughout would improve clarity.

BPS: As discussed in a previous comment, we will change the main text units to depth (mm/day), which will be consistent with the units in Table S1.

Table S2: for leaf conductance and water potential at 50% reduction of conductance, I would specify that these parameters refer to stomatal closure, not leaf xylem cavitation.

BPS: We will update the $\psi_{l,50}$ to specify stomatal closure. However, the xylem to leaf conductance ($g_{xl,max}$) does represent xylem cavitation, which we will emphasize in the text.

Eq. S3: I am not sure why this metric was also normalized by the "relative soil saturation of soil water stress", or difference between theta_o and theta_c. It would also be useful to remind the reader of the meaning of these moisture thresholds.

BPS: This normalization was to control for differing ranges of soil water content experience by soil plant systems with differing soil water characteristic parameters. We will reiterate that θ_o and θ_c are the incipient and complete water content for stomatal closure ($\psi_{l,o}$ and $\psi_{l,c}$ mapped to water content). Overall, this normalization does not affect the main result of estimating a threshold for transport-limitation.

Section S6.2.1: is LAI in this section the total LAI?

BPS: Yes, we will clarify this in the updated version

L203: by “diffuse leaves” is it meant “shaded leaves”?

BPS: Yes, thank you for catching this typo. We will update this to shaded.

L205: “value” singular.

BPS: Thank you, will update.

L321: in Medlyn’s model, transpiration is minimized for given photosynthesis; maximizing the ratio of photosynthesis and transpiration would not be a well-posed problem (for stomatal conductance going to zero, the photosynthesis-to-transpiration ratio is highest).

BPS: Thank you for this clarification, we will reflect this in the update.

L322: another assumption is that leaves are optimized for light-limited conditions, not CO2 limited.

BPS: We will include this in the updated manuscript.

L358: I see the rationale for keeping the gas exchange model (relatively) simple, but could this assumption affect the results? Temperature effects on photosynthetic parameters will affect stomatal conductance via Medlyn’s model and ultimately water demand as well.

BPS: Yes, this assumption could affect the magnitude of our results. However, we believe that our main conclusions on the inadequacy of β to capture transpiration downregulation in transport-limited systems will not change because both the β and PHM models will incur similar errors for neglecting temperature dependence. We will add further discussion of this issue to the revised supplement.

L367: typo “differ from”.

BPS: Thank you, will update.

L372: typo “is given”.

BPS: Thank you, will update.

Section S6.4.3: it would be good to provide a clarification that the equations used to account for the leaf nitrogen profile do not assume a dynamic sub-daily allocation scheme (nitrogen cannot be re-allocated so quickly in the canopy), but are the result of integration of the vertical profile of a given photosynthetic parameter, so that the proportion of nitrogen in shaded or sunlit leaves changes during the day, but not the actual leaf nitrogen concentration at any given depth in the canopy (assuming I am interpreting correctly the equations in this section).

BPS: Yes, your interpretation is correct. We will clarify this assumption in Sect. 6.4.3 to avoid any confusion.

L385: typo “leaves”.

BPS: Thank you, will update.

Eq. S86: assuming vertically uniform hydraulic conductivity and sapwood area.

BPS: Yes, we will explicitly state this assumption.

Eq. S89: assuming 1-dimensional transport in the soil, as in the xylem?

BPS: Yes, we will explicitly state this assumption.

References

DeLucia, E.H., Heckathorn, S.A., 1989. The effect of soil drought on water-use efficiency in a contrasting Great-Basin desert and Sierran montane species. Plant Cell Environ. 12, 935–940.

Domec, J.C., Pruyn, M.L., 2008. Bole girdling affects metabolic properties and root, trunk and branch hydraulics of young ponderosa pine trees. Tree Physiol. 28, 1493–1504.

Maherali, H., DeLucia, E.H., 2000. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. Tree Physiol. 20, 859–867.

Stout, D.L., Sala, A., 2003. Xylem vulnerability to cavitation in Pseudotsuga menziesii and Pinus ponderosa from contrasting habitats. Tree Physiol. 23, 43–50.