Dear Dr. ten Veldhuis,

We thank you for the opportunity to submit our revisions for *Plant Hydraulic Transport Controls Transpiration Sensitivity to Soil Water Stress* (hess-2020-671) to HESS for further review. We have addressed the thoughtful and thorough comments from all reviewers in the attached revised manuscript and supplement. Additionally, we have included a line-by-line response to reviewer comments as well as a track-changes manuscript per your request.

We have listed below the main changes to figures and sections in the revised manuscript based on reviewer comments and our discussions to further clarify and contextualize our message. Do not hesitate to contact us for additional information or materials.

Figure Changes:

- We have added an additional figure (Fig. 1) to explain minimalist and complex PHM and beta model structure at the request of Reviewer #3. We have re-numbered Figs. 1-4 as Figs. 2-5.
- We have changed the units in Figs. 2-5 and throughout the paper from energy (W/m^2) to depth (mm/day) to reach a broader hydrological audience at the behest of all reviewers.
- We have updated the LSM calibration procedure, resulting in updates to Figs. 4-5.

Main Text Changes:

- Sect. 2.1-2.2: Extensive edits include the incorporation of the new Fig. 1, updating units and clarifying assumptions about leaf vapor transport. Additionally, we have re-ordered text so that minimalist and complex PHM formulations mirror one another.
- Sect. 2.3: We have added additional text to explain our updated calibration procedure based on the comments from Reviewer #3.
- Sect. 2.4: We have added significant text justifying the subsurface moisture data used to force the LSM based on comments from Reviewer #1 and #2
- Sect. 2.5: We have elaborated on common beta models and justified our specific formulation in response to all 3 reviewers.
- Sect. 3.1: We have re-arranged the text to more clearly align with Fig. 2.
- Sect. 3.2: To improve clarity, we have split the discussion on drivers of differences in PHM and beta into separate paragraphs and highlighted behaviors that occur in the later LSM analysis.
- Sect. 3.3: We have removed redundant information covered in the Sect. 2 and have slightly modified text order for clarity.
- Sect. 4: We have added a paragraph on how more detailed representation of plant physiology could affect our results.

Sincerely,

Brandon Sloan

Sally Thompson

Xue Feng

<u>Author Response to Reviewer Comment Set #1</u>

<u>General comments:</u>

The manuscript tests and compares various empirical correction functions (β) of stomatal closure under soil-moisture limitations to more advanced plant hydraulics models. The authors explain the source of the differences between the β and mechanistic plant hydraulics approaches, leading to the development of a new dynamic β model that compares well to mechanistic plant hydraulic schemes, but with half the parameters. The authors are clearly well aware of the issues within terrestrial biosphere models. This is a nice manuscript. The supplementary information is particularly clear and thorough.

<u>Major comments:</u>

(1) A key strength of the manuscript is that it proposes a new dynamic β scheme which has half the parameters as the full plant hydraulics scheme. This is mentioned in the main text beginning at line 306 and more fully discussed in the SI (lines 40-44). The simplicity of the parameterization should be more fully discussed in the main text, considering its importance and since it seems to have at least partially motivated the study (as discussed in introduction; lines 49-54). The parametric benefits of the new scheme should be brought out more in the title (which is appropriate, but does not reflect this strength– if anything, the current title evokes an obvious statement), the abstract (which mentions the scheme being generally parsimonious but without being exact), and the end the introduction (near lines 58-59).

Response: Thank you for the comment. We are currently working on a follow-up manuscript to validate the simple parametrization for the dynamic β and to relate the parameters to measurable hydraulic traits. The main focus of the current paper was to identify the spectrum of transport-limitation, recognizing that the coupling of soil water supply to atmospheric moisture demand through leaf water potential is why β and PHMs differ. The dynamic β emerged as a by-product of this theoretical understanding. Therefore, we are still working through whether we can generalize this for all transport-limited sites consisting of various soil and plant hydraulic properties, and reserve additional analysis on the dynamic β model for future work.

Nevertheless, we have emphasized in the updated manuscript that the dynamic β is a potentially more parsimonious alternative to PHMs and highlight the current benefit of reduced computational cost as well as the future work needed to generalize to all transport-limited sites. We briefly mention the potential for the method in <u>Lines 15,66-67</u>, while providing more detailed discussion in <u>Lines 343-348</u> in Sect. 3.3 and <u>Lines 399-402</u> in Sect. 4.

(2) It should be made clear that the results and their interpretation reflect β functions when formulated as a function of soil water potential (or soil moisture content by extension). The choice of soil water potential as the explaining variable is explained in lines 158-164, but should be discussed elsewhere for emphasis. It is not clear if the manuscript's conclusions would be the same had the authors formulated β as a function of leaf water potential, which is recognized as an alternative model scheme in line 159. I expect that the conclusions would be different had β been defined as a function

of leaf water potential, considering that the finite plant conductance is explained here as a controlling variable for the response (lines 211, 252-257, 290), and the conductance would be reflected in the resulting leaf water potential. Whether or not the conclusions would be different for a leaf potential formulation, at the very least, these concepts should be explained in the text. Nonetheless, regardless of the alternative formulations for β and their implications, the study is still highly meaningful to terrestrial biosphere models, considering most terrestrial biosphere models apply β as a function of soil water potential or moisture – another point that can be further brought out in the text (or a Table could summarize existing schemes in terrestrial biosphere models).

Response: Thank you for the comment. Based on your comment, we realize now that saying β is formulated as a function of leaf water potential is not quite correct. Originally, we referenced Jarvis (1976) for this point as he does use an empirical downregulation term as a function of leaf water potential. However, he provided a simple PHM to calculate leaf water potential from soil water potential. The older TBMs that had used the Jarvis formulation (mainly SiB2) effectively transformed soil moisture to leaf water potential. Therefore, we have removed mention of β formulations as a function of leaf water potential from Sect. 2.5.

Additionally, we have updated Sect. 2.5 to clarify that β is typically defined in terms of soil moisture (using either soil water potential or soil water content), which avoids calculating leaf water potential (<u>Lines 202-205</u>). We also direct the reader to Trugman et al. (2018) in <u>Lines 205-206</u>, where there is a nice summary table of typical β formulations in TBMs (as functions of soil water potential and soil water content) in lieu of creating our own table.

Your comment also brings up another important point worth clarifying: do our results extend to β functions using soil water content instead of soil water potential? We selected β in terms of soil water potential for a few reasons. Primarily, soil water potential provides more consistent comparison with PHMs as water transport follows a water potential gradient and not a water content gradient. Additionally, Egea and Verhoef (2011) found β using soil water content struggled to match empirical data, unless a more complex functional form was used---likely accounting for the nonlinear mapping between soil water content and soil water potential. We have added to Sect. 2.5 to justify our use of soil water potential (<u>Lines 215-218</u>) and clarify the conditions under which our results apply to β using soil water content (<u>Lines 213-214</u>).

<u>Minor comments:</u>

(3) Line 17: "water use" is a broad term that can mean many things besides transpiration. To be more exact, change "water use" to "transpiration."

Response: Agreed, we have addressed in <u>Line 17</u> of the updated manuscript.

(4) Eq. 3 + 8: These formulations are reasonable enough for the purposes of the study; however, limitations of these formulations should be explained. Eq. 3 is flawed in the sense that there is no unique stomatal conductance response for a given leaf water potential (recently discussed by Anderegg & Ventuas, 2020; "Plant hydraulics play a critical role in Earth system fluxes"). Similar logic applies to Eq. 8. The formulation for stomatal conductance as calculated by Eq. 8-9 is a little funny, considering at least two things. First, Eq. 8-9 causes the minimum stomatal conductance to decline with leaf water potentials. And second, g1 in Eq. 9 is considered a constant, even though it reflects

the marginal water use efficiency (which is recognized by the authors in the SI; lines 325-326), which can be further considered a function of leaf water potential (e.g. Manzoni et al., 2011; “Optimizing stomatal conductance for maximum carbon …”; Wolf et al., 2016; “Optimal stomatal behavior with competition for water and risk of hydraulic impairment”). I do not expect these equations to change with revision, but the formulations should be justified in the text or SI.

Response: This is a very interesting issue, which we attempt to address as follows. Figure 2 in Anderegg & Venturas (2020) illustrates the non-unique response of stomatal conductance to leaf water potential (shown below in Fig. RC1a). Our formulations of stomatal downregulation in response to water potential, $f(\psi_l)$, exhibit similar non-uniqueness. This is because Eq. 3 (and Eq. 8) does not relate actual stomatal conductance to leaf water potential, but rather relates actual stomatal conductance <u>normalized by the well-watered value</u> to leaf water potential (shown in Fig. RC1b inset for Eq. 8). So even with this simple formulation, the relationship between stomatal conductance and leaf water potential varies with VPD (Fig. RC1b) because the well-watered stomatal conductance value (determined by the Medlyn equation) changes with environmental forcings. To illustrate this, we quickly ran our LSM with PHM downregulation scheme for parameters and environmental conditions similar to those in Venturas et al. (2018). Fig. RC1b illustrates that our simple Jarvis-like term can produce similar results to those in Anderegg and Venturas (2020), though we do agree there are benefits to the Venturas et al (2018) formulation in terms of $f(\psi_l)$ being an emergent property of measured traits. However, for the purpose of this work, our assumptions should be sufficient.

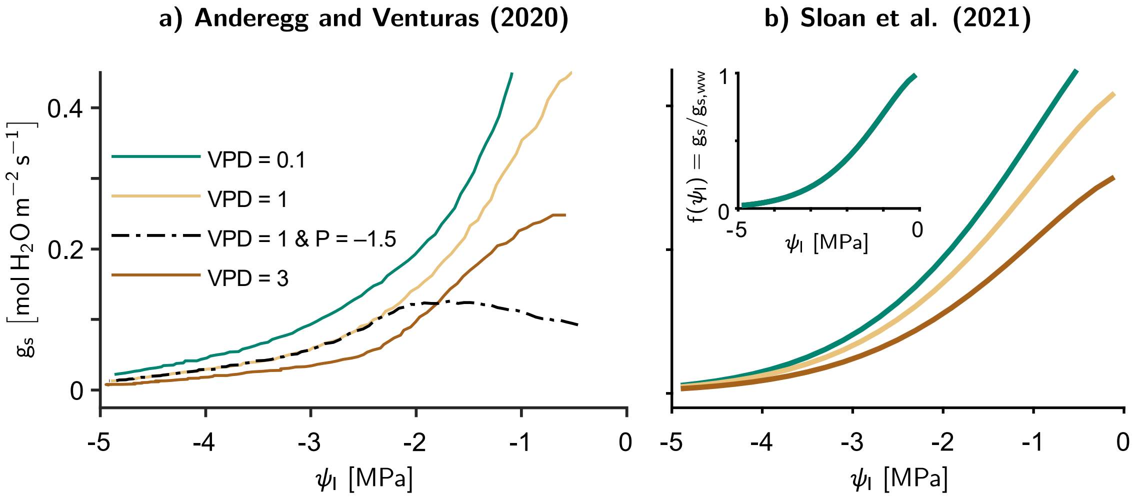

Figure RC1: a) Figure 2b taken (and modified) from Anderegg and Venturas (2020) illustrating the non-unique relationship between stomatal conductance (g_s) and leaf water potential (ψ_l). b) Results for our PHM transpiration downregulation scheme using similar parameters and environmental forcings to Fig. 2a. We obtained relevant parameters from Venturas et al. (2018) for Aspen, and made educated guesses on others that were not explicitly in the formulation Venturas et al. (2018) (e.g., Medlyn’s g_1). The point of the figure was not to match exactly Anderegg and Venturas (2020), but rather to show our model creates the non-unique g_s- ψ_l behavior and could match the Fig. 2a behavior with tuning (except the dashed line representing no xylem refilling). Our scheme utilizes a normalized curve (inset) of g_s to its well-watered value ($g_{s,ww}$) to represent stomatal closure, rather than this relationship being an emergent property of plant hydraulic properties and an optimality hypothesis as in Venturas et al. (2018).

In order to clarify our approach and the importance on your point on the non-unique g_s- ψ_l relationship, we have updated the minimalist PHM demand paragraph in Sect 2.1 (Lines 87-102). Firstly, we explicitly state that our approach is similar to Jarvis and creates the non-unique relationship g_s- ψ_l highlighted by Anderegg and Venturas (2020) in Lines 100-102. Furthermore, we have updated the $f(\psi_l)$ equations (Eq. 3 and 13) to show they represent $g_s(\psi_l)/g_{s,ww}$ with our Jarvis assumption. These points are echoed in Lines 149-151 of Sect. 2.2.

In response to the comments on Eqs. 8-9 (now Eqs. 13 and 12, respectively), we selected this Jarvis-like approach because it allows for simple comparison between the minimalist and complex PHM formulations as well as β. As you have pointed out, this approach is similar, but not identical to the approaches of Manzoni et al. (2011) and Wolf et al. (2016). As mentioned in the previous paragraph, we have clarified that our Jarvis-like approach is a simplification that facilitates our model comparisons (Lines 102 and 150). Furthermore, we have added discussions to Sect. 2.5 (Lines 206-209) that cites other established methods for applying β or $f(\psi_l)$ to stomatal conductance. We explain that our main conclusions on the differences between PHMs and β will not change with different stomatal downregulation formulations, as long as the downregulation factors from each model are applied consistently (Lines 210-213).

(5) Lines 154-156: This sentence is vague, and the intent is unclear. In particular, ”tested against the selection of different soil moisture depths to represent plant water availability” suggests to me something about parameterized rooting depths and/or soil properties, but again, it is unclear. If it concerns rooting depth, refer to the SI (either generally to section S6.5.3 or specifically to Eq. 84). However, the rooting depth appears to have been set as a constant based on literature review (Table S7) and not a calibrated value. As a side note, the rooting depth of 0.1 m seems very shallow for an 18 m tall pine tree.

Response: Thank you for pointing this out. We have significantly revised Sect. 2.4 (Lines 188-200) based on this comment and a comment from Reviewer 2 by adding more details from Sect. S4 (now Sect. S5) justifying our use of soil moisture measurements at 50 cm to force the model. We selected this depth based on analyzing GPP deviations from the mean as a function of dryness (explained now in Lines 193-197).

Thank you for catching the typo for rooting depth. The rooting depth should have a value of 1.1 m based on a previous modeling study at US-Me2 from Schwarz et al. (2004). We have updated supplemental materials (Table S4) and added reference to the rooting depth in Line 197.

(6) Line 169: Refer to Figure S2 here. Figure S2 helps explain the linear functions used by the dynamic β scheme.

Response: We have added reference to Fig. S2 (currently Fig. S10 after Supplement re-arrangement) in Line 225.

References for Response to Reviewer 1

Anderegg, W. R. L., & Venturas, M. D. (2020). Plant hydraulics play a critical role in Earth system fluxes. *New Phytologist*, *N/A*, 4. https://doi.org/10.1111/nph.16548

Egea, G., Verhoef, A., & Vidale, P. L. (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. https://doi.org/10.1016/J.AGRFORMET.2011.05.019

Jarvis, P. G. (1976). *The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field*. *Trans. R. Soc. Lond. B* (Vol. 273).

Manzoni, S., Vico, G., Katul, G., Fay, P. A., Polley, W., Palmroth, S., & Porporato, A. (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. https://doi.org/10.1111/j.1365-2435.2010.01822.x

Venturas, M. D., Sperry, J. S., Love, D. M., Frehner, E. H., Allred, M. G., Wang, Y., & Anderegg, W. R. L. (2018). A stomatal control model based on optimization of carbon gain versus hydraulic risk predicts aspen sapling responses to drought. *New Phytologist*, *220*(3), 836–850. https://doi.org/10.1111/nph.15333

Wolf, A., Anderegg, W. R. L., & Pacala, S. W. (2016). Optimal stomatal behavior with competition for water and risk of hydraulic impairment. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(46), E7222–E7230. https://doi.org/10.1073/pnas.1615144113

Author Response to Reviewer Comment Set #2

The study analysed the impact of heuristic β-type water stress formulations, commonly adopted to many land-surface schemes in terrestrial biosphere models and identifies when such a formulation diverges for more detailed models that include explicit formulation of plant hydraulics. Additionally, it proposed a new dynamic β -type formulation that "emulates" with a very reduced complexity the limitations that originate from plant hydraulics. The study is focused and very well written, and clearly within the scope of HESS. I found particularly insightful the analysis with the simple plant hydraulic model that clearly shows when plant hydraulics are expected to play a major role, and the dynamic β model which can be easily adopted by exiting TBMs. I can suggest the manuscript for publication after the following comments have been addressed:

Major comments

(1) I believe that information from S4 should move to the main manuscript. While reading the manuscript I was confused whether soil moisture dynamics were simulated, or if soil moisture and soil water potential were set to the observed values at the site. I could also not tell what ψs corresponds to (i.e. root zone average potential? potential of root average soil moisture?). I appreciate that the authors like to present a focused manuscript, but bringing this information in the main article will improve its readability.

Response: Thank you for the comment. Following this and a similar comment from Reviewer 1, we have updated Sect. 2.4 (Lines 188-200) to include additional details from Sect. S4 (now Sect. S5) explaining the use of soil moisture measurements at 50 cm to force the model. We selected this depth based on analyzing GPP deviations from its mean as a function of dryness (explained now in Lines 193-197).

In regards to your second question, ψ_s is the root zone average soil moisture. We have updated Sect. 2.1-2.5 to clearly reflect this definition (Lines 81,129, and 193).

(2) Regarding the calibration of the dynamic β model, to my understanding, the results from the full complexity PHM was used to derive the dependence of the stress factor to Tww and ψs. As this would not be the case with existing TBMs, can the authors suggest a general procedure on how a generic calibration could be achieved for a "general-purpose" dynamic β model?

Response: We are currently working on a follow-up manuscript to validate the simple parametrization for the dynamic β and to relate its parameters to key hydraulic traits. In the updated manuscript, we emphasize that the dynamic β has potential to be a parsimonious alternative to PHMs and that we are pursuing future work on the topic (Lines 15,66-67, 343-348, 399-402).

Currently, our dynamic β formulation can provide less computational complexity than a PHM (Lines 343-348); however, we do not yet know if the simple linear parameter relationships (Fig. S12) will hold for sites other than US-Me2. A user could attempt calibration with our model structure as is, but further work must be done to ensure its general applicability. We highlight these needs in Lines 399-402.

(3) One aspect worth discussing is the use of capacitance within a plant hydraulic model. I would encourage the authors to expand their discussion regarding this point, as several TBMs now adopt a resistor/capacitor approximation when formulating their plant hydraulic modules.

Response: Thank you for pointing this out. In the updated manuscript, we discuss the potential effects of incorporating plant capacitance in Sect. 4 (Lines 371-375). We expect plant capacitance to cause hysteresis in the PHM transpiration downregulation patterns, which would be very difficult for existing β formulations to capture. However, we expect for supply-limited systems that water potential will equilibrate quickly (due to high conductance) and the hysteretic effects may be negligible. Therefore, we think that adding capacitance would: 1) increase the divergence between PHMs and β for transport-limited systems and 2) have little impact in supply-limited systems.

(4) I agree with reviewer 1 regarding the interpretation of the results. The behaviour of β models limiting particularly photosynthetic rates (or in some cases Vcmax), might have a different behaviour that the reported. That would be worth discussing further.

Response: This is an interesting point. We have updated Sect. 2.5 (Lines 206-209) to discuss the debate over whether to apply β directly to stomatal conductance and/or to non-stomatal limitations (as you have mentioned). We emphasize that our main conclusions about the differences in β and PHMs will not change as long as the downregulation factors for β ($\beta(\psi_s)$; Eq. 15-16) and PHMs ($f(\psi_l)$; Eq. 3,13) are applied consistently to the same variables in the downregulation scheme (Lines 210-214). For example, if both $\beta(\psi_s)$ and $f(\psi_l)$ were applied to V_{cmax}, the coupling between atmospheric moisture demand and soil water stress is still expected to disappear as conductance becomes infinite, because ψ_l approaches ψ_s. Therefore, PHMs would still approach β. The only changes may be the magnitude of differences in the LSM analysis for a transport-limited site.

Minor comments

(5) Line 101, 98: has instead of is?

Response: Since I am defining the terms, I think "is" is actually the appropriate form.

(6) Line 133: Neutral atmosphere, instead of "negligible atmospheric stability"

Response: We have changes in Line 165 of the updated manuscript.

(7) Line 137: "and codes will be made available online with acceptance of this manuscript". Not a necessary statement in the manuscript. The code will appear upon acceptance.

Response: We have removed this in the updated manuscript.

(8) It would be nice to keep consistent units for transpiration and conductance terms throughout the manuscript.

Response: I think this comment is referring to Equation 9 and stomatal conductance in terms of moles/m^2/s. Based on a comment from reviewer 3, we have updated all units to ensure consistency between minimalist and complex formulations. See track changes document for changes as they occur through the entire document and figures. The changes to units will be as follows:

- **Change transpiration fluxes from W/m^2 to mm/day.**
- **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.**

Author Response to Reviewer Comment Set #3

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

(1) 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.

Response: 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 (now Eq. 11) 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 have made the following unit changes listed below. These changes are not listed as they occur throughout the paper, but are shown in the track changes manuscript at the end of this document. The changes to units will be as follows:

- **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 (see Eq. 11 in updated manuscript.).**

(2) 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?

Response: 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 6 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. RC2a). This parameter adjustment had negligible impact on the overall LSM performance (Fig. RC2b) because the LSM suffers from equifinality (i.e., multiple parameter sets give similarly match observations). 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.

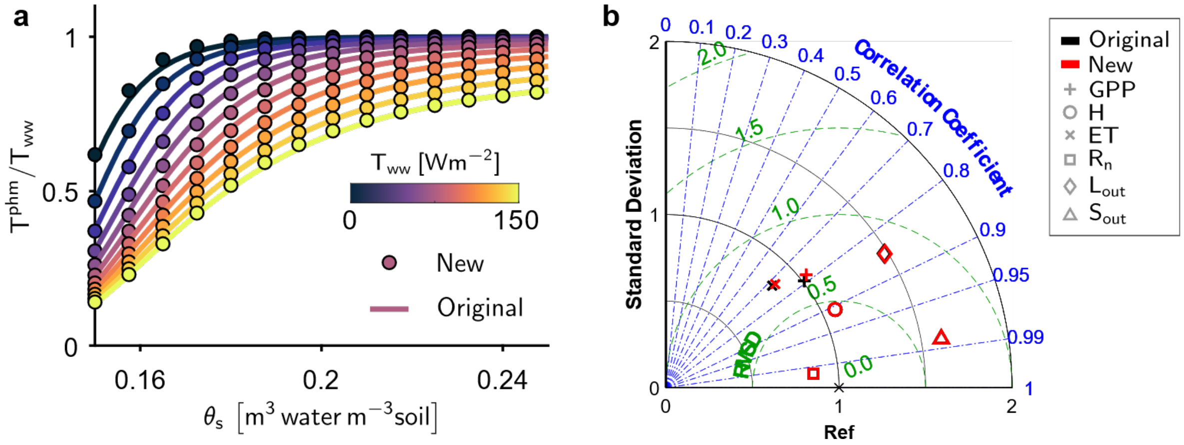

Figure RC2: a) Comparison of the transpiration downregulation for the original calibrated LSM parameters (solid lines) to the newly updated parameters (filled circles) in Table RC 1. The parameters closely replicate the downregulation behavior of the original parameters while provding more realistic 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 have updated Figs. 3-4 (now Figs. 4-5) with these new LSM results and detail additional calibration steps in Sect. 2.3 (Lines 175-180). Furthermore, we have added additional text (Lines S391-S442) and incorporated Table RC1 (Table S6) and Figure RC2 (Fig. S4) in the supplement to help explain our method.

(3) 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.

Response: 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 have replaced the term 'supply-limited' with 'soil-limited' in the updated manuscript (Line 260 and elsewhere). 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 elaborate in the discussion that beta represents soil-limited systems because soil water status is an adequate proxy for leaf water status (Line 366-367).

Minor main text comments

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

Response: We like this idea and have implemented a two-panel figure (Fig. 1 in updated manuscript) showing β and PHM model structure differences across the complex and minimalist versions.

(5) 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?

Response: Yes, we mean the latter. In Line 28-29 we state that "β" refers to the downregulation model in this paper whereas "β function" refers to the actual function of soil moisture. We have clarified this statement in the updated manuscript to convey that it is stomatal responses from TBMs using the β model that are insensitive to atmospheric dryness (Lines 40-42).

(6) L52: through acclimation as well.

Response: We will add this in the updated manuscript.

(7) 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.

Response: This is a good point and has been added to the updated manuscript (Line 56).

(8) L60: for clarity I would suggest to add "water" in front of "supply-demand framework".

Response: We have added this in the updated manuscript (Line 67).

(9) 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.

Response: This was my misunderstanding. In the updated manuscript, we have removed the citation and explicitly state that we ignore hydraulic limits (<u>Lines 83-85</u>) 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 (<u>Lines 313-319</u>).

(10) L123: how are least squares used in this context?

Response: 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 have clarified this point in <u>Lines 159-160</u> of updated manuscript.

(11) L243: extra "the".

Response: Thank you, have fixed in the updated manuscript.

(12) 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.

Response: 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 (we call this the downregulation envelope) depending on data or assumed parameters. For example in our LSM analysis, we fit β to mean T_{ww} conditions (Fig. 5a,b in the updated manuscript), 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 downregulation envelope that cannot be adequately described with a single β curve.

In the updated manuscript, we have elaborated further on this point (<u>Lines 308-312</u>) and added light gray shading to Fig. 4b,d,f to illustrate the PHM downregulation envelope. Hopefully this will drive home the point that β cannot adequately capture the range of PHM behavior.

(13) 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))?

Response: 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. S5) that contribute as well to the bias.

(14) 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.

Response: We received similar comments from Reviewers 1 and 2. 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 have updated the manuscript to emphasize the dynamic β has potential be a parsimonious PHM replacement given its reduced computational demand (Lines 345-348) and similarity to current β frameworks (Lines 393-398). However, we state the dynamic β must be calibrated to site-specific data and its generalization is the topic of future work (Lines 398-402*).*

Minor comments for the Supplement

(15) 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.

Response: We have re-ordered the Supplement to follow more closely the order the main text. The re-ordered Supplement using the original section names as follows: S1, S6, S7, S5, S4, S2, S3.

(16) 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.

Response: As discussed in a previous comment, we have changed the main text units to depth (mm/day), which is now consistent with the units in Table S7-S8 (previously Table S1).

(17) 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.

Response: We have updated the $\psi_{l,50}$ to specify stomatal conductance. However, the xylem to leaf conductance ($g_{xl,max}$) does represent xylem cavitation, which we have highlighted in the text (Line S280) and added the word xylem to Table S6 (previously Table S2).

(18) 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.

Response: This normalization was to control for differing ranges of soil water content experience by soil-plant systems with differing soil water characteristic parameters. We have re-iterated that θ_o and θ_c are the incipient and complete water content for stomatal closure (Lines S562-S564). Overall, this normalization does not affect the main result of estimating a threshold for transport-limitation.

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

Response: I am unsure what "total LAI" means. We have added text (Lines S42-S44) explaining the LAI is the one-sided leaf area index that is used to scale leaf-scale results to big leaf results. Please us know if this answers your question.

(20) L203: by "diffuse leaves" is it meant "shaded leaves"?

Response: Yes, thank you for catching this typo. We have updated this to shaded (Line S65).

(21) L205: "value" singular.

Response: Thank you, have updated (Line S67).

(22) 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).

Response: Thank you for this clarification, we have updated it (Line S181-S182).

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

Response: We have included this in the updated manuscript (Line S182-S183).

(24) 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.

Response: 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 have added further discussion of this issue to the revised supplement (Line S223-S224).

(25) L367: typo "differ from".

Response: Thank you, have updated (Line S230).

(26) L372: typo “is given”.

Response: Thank you, have updated (Line S234).

(27) 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).

Response: Yes, your interpretation is correct. We have clarified this assumption (Lines S229-230, 235-237).

(28) L385: typo “leaves”.

Response: Thank you, have updated (Line S248).

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

Response: Yes, we have explicitly stated this (Line S281-S282).

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

Response: Yes, we have explicitly stated this assumption (Line S264, S276-S277).

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.