Plant Hydraulic Transport Controls Transpiration Response to Soil Water Stress

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Abstract. Plant transpiration downregulation in the presence of soil water stress is a critical mechanism for predicting global water, carbon, and energy cycles. Currently, many terrestrial biosphere models (TBMs) represent this mechanism with an empirical correction function (β) of soil moisture—a convenient approach that can produce large prediction uncertainties. To reduce this uncertainty, TBMs have increasingly incorporated physically-based Plant Hydraulic Models (PHMs). However, PHMs introduce additional parameter uncertainty and computational demands. Therefore, understanding why and when PHM and β predictions diverge would usefully inform model selection within TBMs. Here, we use a minimalist PHM to demonstrate that coupling the effects of soil water stress and atmospheric moisture demand leads to a spectrum of transpiration response controlled by soil-plant hydraulic transport (conductance). Within this transport-limitation spectrum, β emerges as an end-member scenario of PHMs with infinite conductance, completely decoupling the effects of soil water stress and atmospheric moisture demand on transpiration. As a result, PHM and β transpiration predictions diverge most when conductance is low (transport-limited), atmospheric moisture demand variation is high, and soil moisture is moderately available to plants. We apply these minimalist model results to land surface modeling of an Ameriflux site. At this transport-limited site, a PHM downregulation scheme outperforms the β scheme due to its sensitivity to variations in atmospheric moisture demand. Based on this observation, we develop a new 'dynamic β' that varies with atmospheric moisture demand—an approach that balances realism with parsimony and overcomes existing biases within β schemes.

1 Introduction

Plants control their water use (i.e., transpiration (T)) and CO₂ assimilation by adjusting leaf stomatal apertures in response to environmental variations (Katul et al., 2012; Fatichi et al., 2016). In doing so, they mediate the global water, carbon, and energy cycles. The performance of most terrestrial biosphere models (TBMs) relies on accurately representing leaf stomatal responses in terms of stomatal conductance (gs). Extensive research has established the relationships between gs and atmospheric conditions like photosynthetically active radiation, humidity, CO₂ concentration, and air/leaf temperature (see Buckley and Mott (2013) and references therein) under well-watered conditions, though the specific forms of these relationships vary (Damour et al., 2010). However, representing the dynamics of gs in response to soil water stress remains problematic.
Many TBMs represent declining $g_s$ and, in turn, transpiration reduction (i.e., downregulation) in response to soil water stress with an empirical function of soil water availability. This method, known as $\beta$ (Powell et al., 2013; Verhoef and Egea, 2014; Trugman et al., 2018; Paschalis et al., 2020), reduces transpiration from its peak value under well-watered conditions ($T_{ww}$), i.e., $T = \beta \cdot T_{ww}$, $0 \leq \beta \leq 1$. (We use the term ‘$\beta$’ in this paper to refer to the downregulation model itself, and the terms ‘$\beta$ function’ or ‘$\beta$ factor’ to refer to the empirical function and its values, respectively.) $\beta$ originated as a heuristic assumption when modeling flow around roots in soils (Feddes et al., 1978) and gained widespread use within TBMs and hydrological models due to its parsimonious form.

However, mounting evidence indicates that using $\beta$ in TBMs is a major source of uncertainty and bias in plant-mediated carbon and water flux predictions. Multiple studies have implicated the lack of a universal $\beta$ formulation as a primary source of intermodel variability in carbon cycle predictions (Medlyn et al., 2016; Rogers et al., 2017; Trugman et al., 2018; Paschalis et al., 2020). For example, different $\beta$ formulations among nine TBMs were responsible for 40%-80% of intermodel variability in global gross primary productivity (GPP) predictions (on the order of 3-283% of current GPP) (Trugman et al., 2018). Aside from the uncertainty in functional form, $\beta$ appears to fundamentally misrepresent the coupled effects of soil water stress and atmospheric moisture demand on stomatal closure. Recent work using model-data fusion at FLUXNET sites highlighted that $\beta$ is overly sensitive to soil water stress and unrealistically insensitive to atmospheric moisture demand (Liu et al., 2020). Furthermore, TBM validation experiments have found $\beta$ schemes produce unrealistic GPP prediction during drought at Amazon rainforest sites (Powell et al., 2013; Restrepo-Coupe et al., 2017) and systematic overprediction of evaporative drought duration, magnitude and intensity (Ukkola et al., 2017) at several Ameriflux sites. The apparent inadequacy of $\beta$ has lead to the adoption of physically-based Plant Hydraulic Models (PHMs) in TBMs (Williams et al., 2001; Bonan et al., 2014; Xu et al., 2016; Kennedy et al., 2019; Eller et al., 2020; Sabot et al., 2020).

PHMs represent water transport through the soil-plant-atmosphere continuum via flux-gradient relationships (based on Hagen-Poiseuille flow) and conductance curves (Mencuccini et al., 2019). The implementation of PHMs in several popular TBMs (e.g., CLM, JULES, etc.) has improved predictions in site-specific GPP and evapotranspiration (ET) predictions (Powell et al., 2013; Bonan et al., 2014; Eller et al., 2020; Sabot et al., 2020; Kennedy et al., 2019) as well as soil water dynamics (Kennedy et al., 2019) compared to $\beta$. PHMs also exhibit more realistic sensitivity to atmospheric moisture demand than $\beta$ (Liu et al., 2020). However, these improvements from PHMs come at the cost of an increased number of plant hydraulic trait parameters and computational burden, which can reduce the robustness and reliability of the predictions (Prentice et al., 2015). Additionally, plant hydraulic traits are difficult to constrain: they vary widely across and within species (Anderegg, 2015) and exhibit plasticity through adaptation. Furthermore, the traits are measured at stem, branch or leaf levels, and scaling them to represent stand or ecosystem behavior remains challenging (Feng, 2020). Consequently, modelers continue to rely on $\beta$ as a parsimonious alternative to PHMs (Paschalis et al., 2020).

The relative strengths and weaknesses of $\beta$ and PHMs suggest that informed model selection requires a better understanding of when the complexity of a PHM is justified over the simplicity of $\beta$. This paper informs such understanding by: i) analyzing the fundamental differences between PHMs and $\beta$ and their controlling parameters (Sect. 3.1-3.2), ii) demonstrating the environmental conditions where PHMs outperform $\beta$ (Sect. 3.2-3.3), and iii) leveraging our theoretical insights to create a
new ‘dynamic β’ that captures the realism of PHMs while retaining the simplicity of the original β (Sect. 3.3). To do this, we first analyze a minimalist PHM using a supply-demand framework, then corroborate the results using a more widely-used, complex PHM, and finally perform a case study with a calibrated land surface model (LSM) using β, PHM, and ‘dynamic β’ downregulation schemes.

2 Methods

2.1 Minimalist PHM

Our minimalist PHM analysis (Sect. 3.1-3.2) uses a supply-demand framework that conceptualizes transpiration as the joint outcome of soil water supply and atmospheric moisture demand (Gardner, 1960; Cowan, 1965; Sperry and Love, 2015; Kennedy et al., 2019). In this framework, ‘supply’ refers to the rate of water transport to the leaf mesophyll cells from the soil, into the roots, and through the xylem. ‘Demand’ refers to the rate of water vapor outflux through the stomata, regulated by stomatal response to atmospheric conditions (Buckley and Mott, 2013) and leaf water potential (Jarvis, 1976; Sperry et al., 1998; Klein, 2014; McAdam and Brodribb, 2016; Anderegg et al., 2017) and driven by the transport capacity of the air surrounding the plant.

The minimalist PHM supply ($T_{phm}^s$ [W m$^{-2}$]; Eq. 1) is represented by an integrated 1-D flux-gradient relationship, bounded by soil and leaf water potentials ($\psi_s$ and $\psi_l$ [MPa]) and mediated by the bulk conductance along the flowpath ($g_{sp}(\psi)$ [W m$^{-2}$ MPa$^{-1}$]). Following Manzoni et al. (2014), we assume constant soil-plant conductance ($g_{sp}$) and steady state transpiration to simplify the integral in Eq. 1 to the product of soil-plant conductance and water potential difference from soil to leaf.

The minimalist PHM demand ($T_{phm}^d$ [W m$^{-2}$]; Eq. 2) consists of a downregulation function ($f(\psi_l)$) multiplied by the well-watered transpiration rate ($T_{ww}$ [W m$^{-2}$]). $f(\psi_l)$ represents stomatal closure under low $\psi_l$ (Jarvis, 1976; Klein, 2014) and can take a piecewise linear form (Eq. 3) parametrized by the leaf water potential at incipient ($\psi_{l,o}$) and complete stomatal closure ($\psi_{l,c}$). $T_{ww}$ is the product of well-watered stomatal conductance ($g_{s,ww}$ [W m$^{-2}$ MPa$^{-1}$]) and the vapor pressure deficit ($D$ [MPa$^{-1}$]). For clarity, ‘well-watered’ refers to abundant soil water conditions under which water transport to the leaves maintains $\psi_l$ high enough to avoid stomatal closure; therefore, $T_{ww}$ and $g_{s,ww}$ only depend on atmospheric conditions. In the minimalist analysis, $T_{ww}$ values were selected and not calculated.

$$T_{phm}^s = -\int_{\psi_s}^{\psi_l} \frac{K_p(\psi) d\psi}{z_{\psi_l} - z_{\psi_s}} = -\int_{\psi_s}^{\psi_l} g_{sp}(\psi) d\psi = g_{sp} \cdot (\psi_s - \psi_l) \quad (1)$$

$$T_{phm}^d = f(\psi_l) \cdot g_{s,ww} \cdot D = f(\psi_l) \cdot T_{ww} \quad (2)$$
The steady state transpiration rate for the minimalist PHM \((T^{phm}; \text{Eq. 4})\) is found at the leaf water potential where supply equals demand \((\psi^*_l)\). The equation for \(\psi^*_l\) is derived by equating Eq. 1-2 and solving for \(\psi_l\) (Eq. 5). Equation 5 is substituted into Eq. 1 to yield \(T^{phm}\) (Eq. 4). The full derivation is shown in section S1 of the Supplement.

\[
f(\psi_l) = \begin{cases} 
1 & \psi_l \geq \psi_{l,o} \\
\frac{\psi_{l,c} - \psi_l}{\psi_{l,c} - \psi_{l,o}} & \psi_{l,c} < \psi_l < \psi_{l,o} \\
0 & \psi_l \leq \psi_{l,c}
\end{cases}
\]  

(3)

The LSM analysis in this paper (Sect. 3.3) uses a more complex PHM formulation following Feng et al. (2018). The PHM segments supply into soil-to-xylem and xylem-to-leaf compartments and demand into a leaf-to-atmosphere compartment. The conductance in each compartment consists of a maximum conductance downregulated by a function of water potential. In the supply compartments, the dependence of conductance on water potential represents ‘hydraulic limits’ (Sperry et al., 1998) that arise via (i) the inability of roots to remove water from soil pores at low \(\psi_s\) and (ii) xylem embolism caused by large hydraulic gradients required under low \(\psi_s\) and/or high \(T_{ww}\). The soil-to-xylem conductance \((g_{sx}[\text{W m}^{-2} \text{MPa}^{-1}]); \text{Eq. 6})\) is its maximum value \((g_{sx,max})\) downregulated by the unsaturated soil hydraulic conductivity curve (Clapp and Hornberger, 1978) which is parametrized by the saturated soil water potential \((\psi_{sat})\), soil water retention exponent \((b)\), unsaturated hydraulic conductivity exponent \((c = 2b+3)\), and a correction factor \((d = 4)\) to account for roots’ ability to reach water (Daly et al., 2004). The xylem-to-leaf conductance \((g_{xl}[\text{W m}^{-2} \text{MPa}^{-1}]; \text{Eq. 7})\) is its maximum value \((g_{xl,max})\) downregulated by a sigmoidal function (Pammenter and Willigen, 1998) which is parametrized by the vulnerability exponent \((a)\) and the xylem water potential \((\psi_x)\) at 50% loss of conductance \((\psi_{x,50})\). The \(g_{sx,max}\) and \(g_{xl,max}\) values are estimated using trait-based equations following Feng et al. (2018) (see section S6 of the Supplement).

\[
g_{sx}(\psi) = g_{sx,max} \cdot \left( \frac{\psi_{sat}}{\psi} \right)^{\frac{c-d}{b}}
\]  

(6)
The single demand compartment represents leaf-to-atmosphere conductance (Eq. 8) as the stomatal conductance ($g_s$; Eq. 8) downregulated from its well-watered value ($g_{s,ww}$) using a Weibull function which is parameterized by a shape factor ($b_l$) describing stomatal sensitivity and the leaf water potential at 50% loss of conductance ($\psi_{l,50}$) (Klein, 2014). This Weibull form is similar to the piecewise linear form of $f(\psi_l)$ in the minimalist PHM (Eq. 3), but is more consistent with formulations common in TBM (Oleson et al., 2018). The $g_{s,ww}$ value (Eq. 9) is estimated by the Medlyn optimal stomatal conductance model (Medlyn et al., 2011) which is parameterized by the minimum stomatal conductance ($g_o$ [mol H$_2$O m$^{-2}$ s$^{-1}$]), Medlyn slope parameter ($g_1$ [Pa$^{0.5}$]), vapor pressure deficit ($D$ [Pa]), net CO$_2$ assimilation rate ($A_n$ [mol CO$_2$ m$^{-2}$ s$^{-1}$]), partial pressure of CO$_2$ at the leaf surface ($c_s$ [Pa]), and atmospheric pressure ($P_{atm}$ [Pa]). We refer the reader to section S6 and S7 of the Supplement for full details and parameter values.

$$g_{xl}(\psi) = g_{xl,max} \cdot \left[ 1 - \frac{1}{e^{a(\psi - \psi_{x,50})}} \right]$$  

(7)

The steady-state solution of the complex PHM requires finding the leaf ($\psi^*_l$) and xylem water potential ($\psi^*_x$) that balance transport in the three compartments. To calculate supply in each compartment ($T_{s,sx}$ and $T_{s,xl}$), we use a Kirchhoff transform to account for conductance varying with water potential along the flow path (Eq. 10) (Sperry et al., 1998) and take the difference in the matric flux potential ($\Phi$) at the segment endpoints (Eq. 11-12). The demand ($T_d$; Eq. 13) is the stomatal conductance scaled by leaf area index (LAI) and multiplied by $D$. The values of $\psi^*_l$ and $\psi^*_x$ that balance flow in each compartment are found using nonlinear least squares. The single big-leaf formulation outlined here has been extended to a two-big leaf formulation used in the LSM analysis (see section S6 of the Supplement for full details). Equations 11-13 contain constants for the latent heat of vaporization ($L_v$ [J kg$^{-1}$]), density of water ($\rho_w$ [kg m$^{-3}$]), density of air ($\rho_a$ [kg m$^{-3}$]), molar density of an ideal gas ($\rho_m$ [mol m$^{-3}$]), and the ratio of molar weight of water to air ($\varepsilon$) to convert transpiration fluxes to units of W m$^{-2}$.

$$\Phi(\psi) = \psi \int_{-\infty}^{\psi} g(\psi') d\psi'$$  

(10)

$$T_{s,sx} = [\Phi_{sx}(\psi_s) - \Phi_{sx}(\psi_x)] \cdot \rho_w \cdot L_v$$  

(11)

$$T_{s,xl} = [\Phi_{xl}(\psi_x) - \Phi_{xl}(\psi_l)] \cdot \rho_w \cdot L_v$$  

(12)
\[ T_d = LAI \cdot g_s \cdot D \cdot \frac{L_v \cdot \rho_a \cdot \rho_m \cdot \varepsilon}{P_{atm}} \]  

(13)

### 2.3 LSM Description and Calibration

The LSM created for this work (Sect. 3.3) is a dual-source, 2-big leaf approximation (Bonan, 2019) adapted from CLM v5 (Oleson et al., 2018) with several key simplifications: 1) steady-state conditions, 2) negligible atmospheric stability, 3) use of the Goudriaan and van Laar radiative transfer model (Goudriaan and Laar, 1994), and 4) forced with soil moisture, soil heat flux and radiative forcing data. Our simplified LSM allowed parallel computation and removal of confounding model structural errors. We refer the reader to section S6 of the Supplement for full model details and justifications. The model was formulated in MATLAB and codes will be made available online with acceptance of this manuscript.

We ran five separate LSMs for this analysis, each with a different transpiration downregulation scheme: 1) well-watered (no downregulation), 2) a single \( \beta (\beta_s) \) with static parameters, 3) a \( \beta \) separately applied to sunlit and shaded leaf areas (\( \beta_{2L} \)) with static parameters, 4) a ‘dynamic \( \beta \) ’ with parameters dependent on \( T_{ww} (\beta_{dyn}) \), and 5) a PHM. We calibrated the LSM with PHM downregulation scheme by simulating 13,600 parameter sets using Progressive Latin Hypercube Sampling (Razavi et al., 2019) on 15 selected soil and plant parameters. The best parameter set was selected by comparison of RMSE, correlation coefficient, percent bias and variance with Ameriflux evapotranspiration, sensible heat flux, gross primary productivity, and net radiation site data. We provide full calibration details in section S5 of the Supplement.

We fit the three LSMs with \( \beta \) schemes to the relative transpiration outputs \( (T/T_{ww}) \) of the calibrated LSM, while the well-watered LSM was run with the calibrated parameters and downregulation turned off. The choice to calibrate a single LSM ensured that the performance differences between the schemes would be due to the PHM representing plant water use more realistically and not to the artifact of differing parameter fits between models. We refer the reader to section S2.2 of the Supplement for specific details of the parameter fits for the \( \beta \) schemes.

### 2.4 Site Description

We selected the US-Me2 “Metolius” Ameriflux site (Irvine et al., 2008) for our modeling case study due to its comprehensive atmospheric and subsurface data availability. The site consists of intermediate-age ponderosa pine on sandy loam soil in the Metolius River Basin in Oregon, USA. Previous modeling (Schwarz et al., 2004) and measured soil parameters and hydraulic traits (Irvine et al., 2008) helped guide calibration. Volumetric soil water content and soil temperature measurements over multiple depths and years enabled the model results to be tested against the selection of different soil moisture depths to represent plant water availability. Full description of the forcing data is given in section S4 of the Supplement.

### 2.5 \( \beta \) Formulations

As mentioned previously, the \( \beta \) transpiration downregulation model does not have a universal formulation. \( \beta \) functions have been heuristically defined using a variety of water supply proxies including \( \psi_l \) (Jarvis, 1976), \( \psi_s \) (Verhoef and Egea, 2014),
and volumetric soil water content ($\theta_s$) (Verhoef and Egea, 2014). Additionally, once the $\beta$ function is selected, the choice remains of where to apply the $\beta$ factor; some TBMx apply the $\beta$ factor directly to $T_{ww}$, whereas others apply it to parameters that control $T_{ww}$, like $g_{s,ww}$ (Kowalczyk et al., 2006) or maximum photosynthetic rates (Zhou et al., 2013; Lin et al., 2018; Kennedy et al., 2019). Here, we have elected to define the $\beta$ function in terms of $\psi_s$ and apply the $\beta$ factor directly to $T_{ww}$ (Eq. 14) as it mirrors the PHM demand equations. In the minimalist analysis (Sect. 3.1-3.2), $\beta(\psi_s)$ (Eq. 15) takes a piecewise linear form (analogous to Eq. 3) which is parametrized by the soil water potential at incipient ($\psi_{s,o}$) and complete stomatal closure ($\psi_{s,c}$). Similarly, in the LSM analysis (Sect. 3.3), $\beta(\psi_s, T_{ww})$ (Eq. 16) takes a Weibull form (analogous to Eq. 8) parametrized by the soil water potential at 50% loss of stomatal conductance ($\psi_{s,50}$) and a stomatal sensitivity parameter ($b_s$). The LSM analysis uses two versions of Equation 16: 1) a static version with constant $b_s$ and $\psi_{s,50}$ (used by the $\beta_s$ and $\beta_{2L}$ schemes), and 2) a dynamic version where $b_s$ and $\psi_{s,50}$ are linear functions of $T_{ww}$ (used by the $\beta_{dyn}$ scheme).

$$T^\beta = \beta(\psi_s) \cdot T_{ww}$$

(14)

$$\beta(\psi_s) = \begin{cases} 1 & \psi_{s} \geq \psi_{s,o} \\ \frac{\psi_{s,c} - \psi_{s}}{\psi_{s,c} - \psi_{s,o}} & \psi_{s,c} < \psi_{s} \leq \psi_{s,o} \\ 0 & \psi_{s} \leq \psi_{s,c} \end{cases}$$

(15)

$$\beta(\psi_s, T_{ww}) = e^{-\left(\frac{\psi_s}{\psi_{s,50}(T_{ww})}\right)^{b_s(T_{ww})}}$$

(16)

3 Results

3.1 $\beta$ as a Limiting Case of PHMs with Infinite Conductance

Looking at the minimalist PHM and $\beta$ models in a supply-demand framework reveals their fundamental differences. The PHM supply lines (red lines in Fig. 1a) illustrate water transport from soil-to-leaf (Eq. 1) at fixed soil water availability ($\psi_s$) with increasing pull from the leaf (lower $\psi_l$). The PHM demand lines (black lines in Fig. 1a) illustrate transpiration rate decline (due to stomatal closure) with lower $\psi_l$ for two atmospheric moisture demands, represented by the well-watered transpiration rate ($T_{ww}$). The intersection of the supply and demand lines in Fig. 1a is the minimalist PHM solution ($T^{\text{phm}}$; Eq. 4) at the leaf water potential ($\psi^*_s$; Eq. 5) that equates supply with demand. The difference between $\psi_s$ and $\psi^*_s$ is the water potential difference ($\Delta \psi$) that drives flow through the soil-plant system mediated by the soil-plant conductance ($g_{sp}$ and slope of supply lines). The minimalist PHM couples the effects of soil water stress to atmospheric moisture demand on transpiration downregulation because leaf water potential ($\psi^*_s$) responds to both $\psi_s$ and $T_{ww}$ until the equilibrium transpiration is reached. The empirical $\beta$ does not readily map to our supply-demand framework since the $\beta$ function is a lumped representation of the soil-plant system.
Figure 1. Fundamental differences between minimalist PHM and $\beta$. a-b, Supply (red) and demand (black) curves for PHM (a, solid lines) and $\beta$ (b, dashed lines) under varying leaf water potentials ($\psi_l$). The squares (circles) represent the PHM ($\beta$) solution — i.e., the $\psi^*_l$ where supply equals demand — for a single soil water availability ($\psi_s$) and two atmospheric moisture demands ($T_{ww}$). These markers carry through panels c and d to illustrate how the solutions between the PHM and $\beta$ diverge at a single $\psi_s$. The relative size of the markers indicates corresponding $T_{ww}$. The water potential difference $\Delta \psi$ required to transport water from soil to leaf is shown in panel a for $\psi_s = -2$ MPa and $T_{ww} = 150$ W m$^{-2}$, c, Solutions of panels a and b mapped to $\psi_s$, where $\Delta T$ is the difference between PHM and $\beta$ transpiration estimates at $\psi_s = -2$ MPa and $T_{ww} = 150$ W m$^{-2}$. d, Relative transpiration, in which solutions in panel c are normalized by $T_{ww}$. The $\beta$ solutions collapse to a single curve, whereas the PHM solutions depend on $T_{ww}$.

185 However, the $\beta$ transpiration rate ($T^\beta$, Eq. 14) decouples the effects of soil water stress and atmospheric moisture demand on downregulation: the $\beta$ function depends only on soil water availability, and $T_{ww}$ depends only on atmospheric conditions.

The coupling inherent to the PHM results in greater transpiration downregulation compared to $\beta$ under the same environmental conditions (Fig. 1c). $\beta$ downregulates transpiration at a fixed proportion based on $\psi_s$ only (i.e., it scales linearly with $T_{ww}$); hence, it can be modeled with a single curve (Fig. 1d). Unlike $\beta$, the PHM downregulates transpiration at a greater proportion with increasing atmospheric moisture demand (i.e., it scales nonlinearly with $T_{ww}$), and thus must be described as a function of both $\psi_s$ and $T_{ww}$. Physically, this result stems from a larger water potential difference ($\Delta \psi = \psi_s - \psi^*_l$), and thus a lower $\psi_l$, required for transport through the soil-plant system under higher atmospheric moisture demand, resulting in greater stomatal closure and thus further downregulation (i.e., smaller transpiration relative to $T_{ww}$ in Fig. 1d).

The physical conditions leading to the empirical $\beta$ assumptions result from supply-demand curves that independently account for the effects of soil water stress and atmospheric moisture demand on transpiration downregulation. This situation only arises when the supply lines are vertical (Fig. 1b), resulting in $\psi^*_l = \psi_s$ and the relative transpiration ($T^\beta / T_{ww}$) collapsing to a single curve (Fig. 1d). Since $g_{sp}$ represents the supply line slope (Eq. 1), $\beta$ is revealed as a limiting case of the PHM in which the soil-plant system is infinitely conductive. We can formally show this limiting behavior in Eq. 17 and 18, where $\psi_s$
approaches $\psi_l^*$ and the difference in PHM and $\beta$ solutions ($\Delta T$) approaches 0 as $g_{sp} \to \infty$. Interpreted this way, the $\beta(\psi_s)$ function (Eq. 15) represents stomatal closure to declining leaf water potential because of its equivalence to $f(\psi_l)$ (Eq. 3) in PHMs. Therefore, a physical interpretation of $\beta$ is transpiration downregulation due purely to stomatal closure as leaf water potentials decline, occurring in an infinitely conductive soil-plant system that causes water potential to remain unchanged between soil and leaf.

$$\lim_{g_{sp} \to \infty} [\psi_l^*] = \lim_{g_{sp} \to \infty} \left( \psi_s \cdot (\psi_o - \psi_c) + \frac{T_{wws} \cdot \psi_s}{g_{sp}} \right) = \psi_s$$

$$\lim_{g_{sp} \to \infty} (\Delta T) = \lim_{g_{sp} \to \infty} (T^{phm} - T^{\beta}) = \lim_{g_{sp} \to \infty} \left( T_{ww} \cdot \left[ \frac{(\psi_{l,c} - \psi_s)}{(\psi_{l,c} - \psi_{l,o})} - \frac{(\psi_{l,c} - \psi_s)}{(\psi_{l,c} - \psi_{l,o})} \right] \right) = 0$$

These minimalist model results suggest that the range of soil-plant conductances ($g_{sp}$) can generate a spectrum of possible transpiration responses to soil water stress. Two classes of behaviors emerge—one in a ‘supply-limited’ soil-plant system, in which $g_{sp}$ is large enough for $\psi_l \approx \psi_s$, thus decoupling the effects of soil water stress and atmospheric moisture demand while allowing the relative transpiration to vary only with $\psi_s$ (Fig. 1d). The other class of behavior arises in ‘transport-limited’ systems with finite $g_{sp}$, in which a non-negligible water potential difference ($\Delta \psi$) is required to transport the water to the leaf, resulting in additional downregulation compared to supply-limited systems (Fig. 1d) and requiring relative transpiration to depend on both $\psi_s$ and $T_{ww}$.

### 3.2 Parameters Controlling the Divergence of $\beta$ and PHMs

The differences in PHM and $\beta$ transpiration estimates ($\Delta T$) depends not only on $g_{sp}$, but also on soil water availability ($\psi_s$), atmospheric moisture demand ($T_{ww}$) and plant water use strategy ($\psi_{l,c} - \psi_{l,o}$) (Fig. 2). Changes in $\psi_s$ are represented by the translation of the supply lines (Fig. 2a,c,e) and result in non-monotonic behaviors in $\Delta T$ over the range of soil water stress ($\psi_{l,c} < \psi_s < \psi_{l,o} + T_{ww}/g_{sp}$) (Fig. 2b,d,f). The peak $\Delta T$ occurs at the incipient point of stomatal closure ($\psi_{l,o}$) because i) when $\psi_s < \psi_{l,o}$, transpiration begins to decrease, and in its extreme limit, transpiration (and thus $\Delta T$) approaches 0 and ii) when $\psi_s > \psi_{l,o}$, the effects of downregulation diminish in both models.

The $\Delta T$-$\psi_s$ non-monotonic behavior inversely scales with $g_{sp}$, as decreasing the soil-plant conductance (and thus increasing transport-limitation) results in flatter supply lines and greater $\Delta \psi$ (Fig. 2a). Furthermore, the range of $\psi_s$ with higher $\Delta T$ increases due to increase in the range of soil water stress for the PHM. The $\Delta T$-$\psi_s$ behavior also scales with atmospheric moisture demand (Fig. 2d) as greater demand line slope results in greater $\Delta \psi$ (Fig. 2c). Lastly, the plant water use strategy ($\psi_{l,c} - \psi_{l,o}$) approximates how sensitive stomatal closure is to $\psi_l$. A more aggressive strategy—closing stomata over a narrower range of $\psi_l$ and $\psi_s$—increases $\Delta T$ as the demand lines becomes more vertical (Fig. 2e). However, this results in a narrower range of soil water stress meaning periods of significant $\Delta T$ may occur infrequently (Fig. 2f). In summary, this analysis suggests that PHMs are most needed to represent transport-limited soil-plant systems under high atmospheric moisture demand.
Figure 2. The effect of soil water potential ($\psi_s$), soil-plant conductance ($g_{sp}$), atmospheric moisture demand ($T_{ww}$) and plant water use strategy ($\psi_{l,o} - \psi_{l,c}$) on differences between the minimalist PHM and $\beta$ models ($\Delta T$). a,c,e, Supply-demand curves at a single soil water availability (indicated by the dark blue x at $\psi_s = \psi_{l,o}$), for three prescribed values of $g_{sp}$, $T_{ww}$, and $\psi_{l,o} - \psi_{l,c}$, respectively. Each parameter ($g_{sp}$, $T_{ww}$, or $\psi_{l,o} - \psi_{l,c}$) is set at 50% above (below) its base values at $g_{sp} = 100$ W m$^{-2}$ MPa$^{-1}$, $T_{ww} = 75$ W m$^{-2}$, $\psi_o = -1$ MPa, and $\psi_o = -2$ MPa using thick (thin) colored lines. The squares (circles) indicate the PHM ($\beta$) solutions, with size corresponding to magnitude of the changing parameter values. Note: the vertical distance between correspondingly sized circle and square is $\Delta T$ and horizontal distance is $\Delta \psi$. b,d,f, The $\Delta T$ results from the panels a, c, and e calculated for a range of $\psi_s$ with line thickness proportional to parameters in the aforementioned panels (e.g., thick blue line in panel b corresponds to 50% increase in $g_{sp}$ shown in panel a). The x-axes are mapped from $\psi_l$ in the top panels to $\psi_s$ in the bottom panels.

variability and moderate soil water stress, especially if downregulation occurs abruptly as a function of soil water stress. The reason PHMs are needed for high atmospheric moisture demand variability is that $\beta$ is empirical and could be fit to observations at differing $T_{ww}$ values. We discuss this point more thoroughly in the Sect. 3.3.

3.3 Improving Transpiration Predictions with a PHM and a ‘Dynamic $\beta$’

We now examine the divergence between PHMs and $\beta$ for a real transport-limited soil-plant system. We calibrated our own land surface model (LSM) mirroring CLM v5 (Oleson et al., 2018) (section S6 of the Supplement) to the surface energy budget
and gross primary productivity (GPP) data at the Ameriflux Metolius ponderosa pine site in Oregon, USA (US-Me2 (Irvine et al., 2008)) for May-August 2013-2014. We use the calibrated LSM to (i) explore the spectrum of transport-limitation in a realistic system, (ii) quantify errors incurred by selecting $\beta$ over a PHM, and (iii) develop and test a new ‘dynamic $\beta$’ that approximates the behaviors of the PHM with two additional parameters to the original $\beta$ function.

Our calibrated LSM uses a more complex formulation of the PHM common to TBMs (Bonan et al., 2014; Kennedy et al., 2019; Williams et al., 2001; Xu et al., 2016; Christoffersen et al., 2016) and ecohydrological models (Sperry et al., 1998; Manzoni et al., 2014) that partitions the soil-plant-atmosphere continuum into soil-to-xylem, xylem-to-leaf, and leaf-to-atmosphere segments, and uses nonlinear (e.g., sigmoidal or Weibull) functions to represent downregulation of segment-specific conductances (Eq. 6-13). This added complexity does not affect the the spectrum of transport-limitation found in the minimalist PHM, shown for the calibrated LSM in an analogous supply-demand framework in Fig. 3. Two main points are worth reiterating. First, soil-plant conductance ($g_{sp}$) controls whether the soil-plant system is supply-limited (high $g_{sp}$; Fig. 3e-f) or transport-limited (low $g_{sp}$; Fig. 3a-b) due to non-negligible water potential differences ($\Delta\psi$), resulting in large differences between PHMs and

**Figure 3.** Transport-limitation spectrum observed in complex PHM formulation. **a,c,e,** Supply-demand curves for three values of soil-plant conductance, $g_{sp}$, using the more complex PHM formulation. Panel c is based on calibrated parameters from the US-Me2 Ameriflux site containing mature ponderosa pines that were determined for the LSM analysis in this paper. Panels a and e contains the calibrated $g_{sp}$ multiplied by 0.1 and 10, respectively. The supply lines (red) are shown at $\psi_s$ equal to 0, -7.5, and -15 MPa and demand lines (black) are shown at $T_{ww}$ equal to 30, 90, and 150 W m$^{-2}$. The PHM solution for $\psi_s$ at -7.5 MPa is shown by the squares with size corresponding to $T_{ww}$ magnitude. **b,d,f,** The relative transpiration for the PHM (solid) in panels a, c, and e and the infinitely conductive $\beta$ solution (dashed line).
\( \beta \) (high \( \Delta T \)) at intermediate \( \psi_s \) values (Fig. 3b,d). Second, for a transport-limited system, \( \Delta T \) increases with higher variability in \( T_{ww} \). To elaborate on this second point, we note that the plotted \( \beta \) function is shown in this case as an upper bound of transport-limited behavior (as \( g_{sp} \to \infty \)). However, in practice, \( \beta \) is an empirical model; depending on how the modeler chooses to fit the \( \beta \) function, it could exist anywhere within the range of the PHM downregulation envelope. Therefore, we must emphasize that the larger range of \( T_{ww} \) results in a greater range of downregulation behaviors from the PHM (Fig. 3b), making a single \( \beta \) increasingly inadequate for capturing the range of behaviors within this downregulation envelope. The consistency in the results based on the minimalist and the more complex PHM suggests that the divergence between PHMs and \( \beta \) in transport-limited systems is not contingent on the linear or nonlinear forms of supply or demand lines, but rather on the existence of a finite conductance itself. Furthermore, these results strongly support the need to use two independent variables, \( \psi_s \) and \( T_{ww} \) (rather than only \( \psi_s \) in \( \beta \)), to capture the coupled effects of soil water stress and atmospheric moisture demand on transpiration downregulation when soil-plant systems are transport-limited.

In light of these findings, we have developed a new ‘dynamic \( \beta \)’ (\( \beta_{dyn} \)) that has an additional functional dependence on \( T_{ww} \) (Eq. 16) and compared it against four other downregulation schemes in this LSM analysis. Thus, the LSM was run using a total of five different transpiration downregulation schemes: 1) well-watered (no downregulation), 2) single \( \beta \) (\( \beta_s \)), 3) \( \beta \) separately applied to sunlit and shaded leaf areas (\( \beta_{2L} \)), 4) \( \beta_{dyn} \), and 5) PHM. The LSM with PHM scheme was calibrated to the Ameriflux data while the \( \beta \) schemes were each fit to the calibrated relative transpiration outputs (\( T^{\text{phm}}/T_{ww} \)) that vary with both \( \psi_s \) and \( T_{ww} \) as previously suggested (Fig. 4a-b). We refer the reader to the Sect. 2.3 for calibration and fitting details.

The median diurnal evapotranspiration (ET) from each LSM is compared to the Ameriflux data for early and late summer 2013-2014 (Fig. 4c-d). During early summer, all models perform similarly due to high soil moisture and minimal downregulation (Fig. 4c). During late summer, soil moisture declines (Fig. S1 of the Supplement), and differences between downregulation schemes emerge. The PHM and \( \beta_{dyn} \) schemes fit the ET observations the best, while \( \beta_{2L} \), \( \beta_s \), and well-watered schemes over-predict ET (Fig. 4d). The sources of bias for the static \( \beta \) schemes are illustrated by plotting the reduction in absolute percent bias between the \( \beta_s \) and PHM schemes (Fig. 4e) for a range of soil (represented by volumetric soil water content, \( \theta_s \ [m^3 \text{ water m}^{-3} \text{ soil}] \)) and atmospheric moisture conditions (represented by \( T_{ww} \)). The PHM provides substantial percent bias reduction relative to the static \( \beta_s \) scheme under soil water stress (\( \theta_s < 0.2 \)) for above- and below-average \( T_{ww} \) values (\( T_{ww} \approx 120 \text{ W m}^{-2} \)). This result is true for both static \( \beta \) schemes (\( \beta_s \) and \( \beta_{2L} \)) because they are fit to the average \( T_{ww} \) at each \( \psi_s \) over the simulation period (Fig. 4a-b). Therefore, as \( T_{ww} \) becomes higher (lower) than the average, these static schemes will overpredict (underpredict) transpiration. The PHM also improves performance during wetter soil conditions (\( \theta_s > 0.2 \)) with high \( T_{ww} \)—which do not represent typical ‘drought’ conditions—suggesting that PHMs are more appropriate than \( \beta \) for representing transpiration downregulation caused by large soil-plant potential differences (\( \Delta \psi \)) under high atmospheric moisture demand. Lastly, the near average \( T_{ww} \) conditions lead to \( \beta \) providing enhanced performance, which can be explained by underlying biases in the calibrated parameter estimates (see Fig. S10 of the Supplement).

Notably, the \( \beta_{dyn} \) downregulation scheme replicates the performance of the PHM scheme by adding a single dimension of \( T_{ww} \) to the original \( \beta \) scheme. The difference in performance between PHM and \( \beta_{dyn} \) schemes is minimal in terms of percent change in bias across all environmental conditions (Fig. 4f), median diurnal variations (Fig. 4a-b), and cumulative
Figure 4. LSM evapotranspiration estimates improved by PHM and new ‘dynamic β’. a-b. Fits of the βs, β2L, and βdyn schemes to the relative transpiration outputs from the calibrated PHM scheme for the sunlit (a) and shaded big leaf (b) of the LSM (see Methods). Note that only three of the infinite family of βdyn curves are shown for illustration. Full fitting details of these three schemes are available in section S2 of the Supplement. c-d. The median diurnal ET estimates for the LSM with five transpiration downregulation schemes compared to Ameriflux observations at the US-Me2 site for early (c) and late summer (d). The dual source LSM calculates ET as the sum of sunlit and shaded big leaf transpiration and ground evaporation. Note: βdyn (red) is overlying PHM (black) results as they are essentially the same. e-f. Reduction in absolute percent bias between the βs and PHM schemes (e) and βdyn and PHM schemes (f) in terms of atmospheric moisture demand (represented by \( T_{ww} \)) and soil water status (represented by \( \theta_s \)). In both plots, blue indicates PHM improvement over the selected β scheme.

4 Discussion and Outlook

The spectrum of transport-limited transpiration highlighted in this work explains why many TBMs that use \( \beta \) to represent transpiration downregulation struggle to predict water, energy, and carbon fluxes under soil water stress (Sitch et al., 2008;...
Powell et al., 2013; Medlyn et al., 2016; Ukkola et al., 2016; Restrepo-Coupe et al., 2017; Trugman et al., 2018) and why implementing PHMs has led to performance improvements (Kennedy et al., 2019; Anderegg and Venturas, 2020; Eller et al., 2020; Sabot et al., 2020). A transport-limited system, characterized by finite soil-plant conductance, leads to a non-negligible water potential difference between the soil and the leaf. It is only when the soil-plant conductance becomes infinite (and the system becomes supply-limited) that leaf water potential approximates soil water potential, and transpiration arises as an independent function of soil water supply and atmospheric moisture demand. These are assumptions inherent to the empirical \( \beta \) and explains why \( \beta \) cannot capture the coupled effects of soil water stress and atmospheric moisture demand. The implications of continued use of \( \beta \) will vary by site. Ecosystems with soil or plant hydraulic properties resistant to flow (e.g., xeric ecosystems, tall trees, species with low xylem conductivity or roots that hydraulically disconnects from the soil during drought) will have large biases depending on the range of soil water availability and atmospheric moisture demand \( (T_{\text{ww}}) \) observed at the site (Fig. 2d and 3b). These errors will not be confined to drought periods, and will also occur during wetter soil conditions (low soil water stress) when atmospheric moisture demand is high (Fig. 2 and Fig. 4e). This is a crucial point, given that ecosystems are projected to experience diverging degrees of VPD stress and soil water stress in the future (Novick et al., 2016). On the other hand, for supply-limited systems (e.g., riparian vegetation, irrigated crops, or groundwater-dependent ecosystems), \( \beta \) may adequately capture transpiration dynamics. Therefore, identifying the combinations of soil parameters and plant hydraulic traits that define transport- or supply-limited systems is an important future step for locating areas around the globe susceptible to prediction error. Our initial estimates indicate a value of soil-plant conductance around \( 10^{3} \text{ W m}^{-2} \text{MPa}^{-1} \) may act as a rough threshold for transport-limitation (see section S3 of the Supplement).

The recognition that a ‘dynamic \( \beta \)’ model can replicate the complexity of a PHM with half the parameters and direct computation (see section S2.2 of the Supplement), simply by adding a dependence on atmospheric moisture demand to the \( \beta \) function, provides a useful pathway for overcoming both the limitations of \( \beta \) and the parametric uncertainties of PHMs (Paschalis et al., 2020; Anderegg and Venturas, 2020). The inadequacies of the static \( \beta \) have been noted since its inception. Feddes et al. (1978), who introduced the first \( \beta \), mentioned \( \beta \)’s dependence on atmospheric moisture demand based on field data (Denmead and Shaw, 1962; Yang and de Jong, 1972) and early plant hydraulic theory (Gardner, 1960). Unfortunately, there have been only a few attempts to rectify these inadequacies in the modeling community, short of implementing a full PHM. For example, Feddes and Raats (2004) updated their original \( \beta \) model to vary the water potential at incipient stomatal closure linearly with atmospheric moisture demand, which has been adopted in the field scale SW AP model (Kroes et al., 2017), while the Ecosystem Demography-2 model (Medvigy et al., 2009) uses a sigmoidal function for transpiration downregulation that contains the ratio of soil water supply to evaporative demand. Within many TBM and hydrological models, a ‘dynamic \( \beta \)’ could easily replace the original \( \beta \) by allowing existing fixed parameters to vary with \( T_{\text{ww}} \) (already calculated in many transpiration downregulation schemes). This would offer a physically-informed alternative to PHMs, with a simpler calibration process. In addition to improving TBM performances, ‘dynamic \( \beta \)’ also has the potential to aid in remote sensing retrievals and indirect inferences of land surface fluxes. Currently, the state-of-the-art ECOSTRESS satellite provides global ET estimates based on a modified Priestley-Taylor formulation that uses a \( \beta \) function to downregulate ET under soil water stress (Fisher et al., 2020). These satellite products could easily implement the ‘dynamic \( \beta \)’ formulation to correct biases for many transport-
limited ecosystems. These potential applications rely on formalizing the relationship between the ‘dynamic $\beta$’ parameters and their dependence on $T_{wtr}$. Further work will focus on linking these relationships to measurable soil properties, plant hydraulic traits, and atmospheric feedbacks.

*Code availability.* The MATLAB code used for the LSM analysis in Sect. 3.3 will be made available upon acceptance of this manuscript. The LSM description is available in section S6 of the Supplement.

*Author contributions.* X.F. and S.T. conceived the idea; B.P.S and X.F. designed the research; B.P.S. performed the research; B.P.S. and X.F. wrote the paper; and S.T. contributed to refining results and revising the paper.

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