Explicit consideration of plant xylem hydraulic transport improves the simulation of crop response to atmospheric dryness in the US Corn Belt

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Abstract

Atmospheric dryness (i.e., high vapor pressure deficit, VPD), together with soil moisture stress, limits plant photosynthesis and threatens ecosystem functioning. Regions where rainfall and soil moisture are relatively sufficient, such as the rainfed part of the U.S. Corn Belt, are especially prone to high VPD stress. With globally projected rising VPD under climate change, it is crucial to understand, simulate, and manage its negative impacts on agricultural ecosystems. However, most existing models simulating crop response to VPD are highly empirical and insufficient in capturing plant response to high VPD, and improved modeling approaches are urgently required. In this study, by leveraging recent advances in plant hydraulic theory, we demonstrate that the widely used coupled photosynthesis-stomatal conductance models alone are insufficient and underestimate VPD stress effects on stomatal conductance and transpiration. Incorporating plant xylem hydraulic transport significantly improves the simulation of transpiration under high VPD, even when soil moisture is sufficient. Our results indicate that the limited water transport capability from the plant root to the leaf stoma could be a major mechanism of plant response to high VPD stress. We then introduce a Demand-side Hydraulic Limitation Factor (DHLF) that simplifies the xylem and the leaf segments of the plant hydraulic model to only one parameter yet captures the effect of plant hydraulic transport on transpiration response to high VPD with similar accuracy. We expect the improved understanding and modeling of crop response to high VPD to help contribute to better management and adaptation of agricultural systems in a changing climate.

1. Introduction

Ecosystems, including agricultural ecosystems for food production, are prone to drought. Drought adversely affects ecosystem functioning and reduces its productivity and crop yield (Dietz et al., 2021; Y. Li et al., 2009). For many years, agricultural drought has been characterized mostly by precipitation shortage and insufficient soil moisture (Alley, 1984; Mishra & Singh, 2010; Palmer, 1965). Recent studies have demonstrated the increasing importance of the adverse effects of atmospheric dryness (high vapor pressure deficit, VPD) on ecosystem productivity, especially for regions where rainfall and soil moisture are relatively abundant (Grossiord et al., 2020; Kimm et al., 2020; Kimberly A. Novick et al., 2016). The U.S. Corn Belt located in the relatively humid Midwestern U.S., which is the world's largest maize and soybean production region, is primarily affected by atmospheric dryness stress compared to soil moisture stress (Kimm et al., 2020). Moreover, VPD is projected to increase globally with increasing temperature under climate change (IPCC Climate Change, 2013). The modeling and understanding of crop response to VPD stress will be increasingly important to any mitigation or adaptation strategies to ensure food production.

However, modeling plant water stress is a major challenge in land surface models, often causing large uncertainties in simulated ecosystem energy, water, and carbon fluxes (Paschalis et al., 2020; Rogers et al., 2017; Trugman et al., 2018). In modern land surface models, a coupled photosynthesis-stomatal conductance model (Ball et al., 1987; Leuning, 1995; Medlyn et al., 2011) combined with a module (Feddes et al., 1976; Sinclair et al., 1984; Venturas et al., 2017) accounting for the effects of plant hydraulic transport on leaf gas exchange is typically used to simulate stomatal conductance and transpiration. The dedicated scheme can be highly empirical (e.g., the empirical soil water stress function, a.k.a., the beta function) or more mechanistic (plant hydraulic models, PHM). Prior studies have demonstrated that despite the coupled-photosynthesis stomatal conductance model capturing part of transpiration response to VPD stress, plant hydraulic transport imposes additional limitations on stomatal conductance under high VPD (Grossiord et al., 2020; Hubbard et al., 2001; Liu et al., 2020; Oren et al., 1999). Meanwhile, the widely used empirical soil water stress function in current-gen and previous-gen

land surface and crop models does not respond to VPD. As a result, the simulation of transpiration response to high VPD stress in many models bears large uncertainties.

Recent advances in plant hydraulic theory and modeling led to the wide incorporation of plant hydraulic transport processes into many land surface models, resulting in better simulations of plant response to water stress overall. Prior studies also demonstrated that PHMs can accentuate the effect of VPD stress (Liu et al., 2020), underlining the necessity of PHMs to accurately capture the full effects of VPD stress on ecosystem functioning, with empirical schemes being mechanistically insufficient. However, to what extent plant hydraulic processes are important in capturing VPD stress under different environmental conditions remains unclear, especially for crops in rainfed regions where the primary water stress factor is VPD. Furthermore, although PHMs provide more mechanistic representations and can theoretically achieve better accuracy, in practice, PHMs have many parameters and are oftentimes difficult to measure and constrain (Anderegg, 2015; Anderegg et al., 2018; Paschalis et al., 2020). This hinders the use of PHMs in many cases where the observation data are scarce or have large uncertainties (Prentice et al., 2015). Therefore, a more comprehensive assessment of the role plant hydraulic processes play in crop response to VPD stress and a simplified representation of the relevant processes would be beneficial for cropland applications.

In this paper, we aim to assess the necessity of plant hydraulic processes in capturing crop transpiration response to high VPD stress and propose a simplified representation of the relevant processes for easier applications. Specifically, we ask two questions: (1) To what extent are plant hydraulic processes important in capturing VPD stress in the U.S. Corn Belt? (2) Is there room for a simplified representation of the plant hydraulic model for simulating crop response to VPD for improved efficiency in model simulation and parameter estimation? To answer the questions, we first do numerical experiments to analyze the theoretical relationship between plant hydraulic processes and the response to high VPD; then we conduct modeling experiments in flux tower sites and compare model simulation with flux tower observations to assess the improvements of incorporating PHM for capturing VPD stress; finally, we introduce a simplified method for simulating VPD stress and demonstrate its effectiveness and efficiency. We expect the improved

understanding of the role of plant hydraulics in the response to VPD stress and the simplified modeling method would contribute to better evaluation and management of agricultural drought under a changing climate.

2. Materials and Methods

2.1 Modeling of crop transpiration response to VPD

2.1.1 Coupled photosynthesis-stomatal conductance model

In modern land surface models, plant transpiration response to water stress is jointly simulated by a coupled photosynthesis-stomatal conductance model and a dedicated scheme to account for water transport in the Soil-Plant-Atmosphere Continuum (SPAC). The response to VPD stress is partially accounted for by the coupled photosynthesis-stomatal conductance model. The widely used Ball-Berry model (Ball et al., 1987) takes relative humidity, which is highly correlated with VPD, as one of the essential environmental factors to determine stomatal conductance. Other similar models such as the Ball-Berry-Leuning (Leuning, 1995) and Medlyn (Medlyn et al., 2011) stomatal conductance models directly use VPD as an input. In all these models, stomatal conductance reduces with rising VPD. In this study, we use the Medlyn stomatal conductance model as stated by

$$g_{s,NHL} = g_0 + (1 + \frac{g_1}{\sqrt{D}})\frac{A}{C_a} \quad (1)$$

where $g_{s,NHL}$ is stomatal conductance (m s^{-1}) with no hydraulic limitation (NHL), g_0 and g_1 are fitted parameters, D is VPD (Pa), A is net CO2 assimilation rate (μmol m^{-2} s^{-1}), and C_a is atmospheric CO2 concentration (μmol mol^{-1}). We will continue using the subscript NHL throughout the article to represent relevant variables that are calculated by the coupled photosynthesis-stomatal conductance model without the constraint caused by plant hydraulic transport in the SPAC, and we refer to the land surface model configured without the constraint of plant hydraulic transport as the NHL model.

2.1.2 Plant hydraulic model

Mechanistically, water transport in the SPAC also responds to VPD and can constrain transpiration when the water transport capability is limited under high VPD (fig. 1b). Many current-generation land surface models use process-based plant hydraulic models as a mechanistic scheme to simulate water transport. Previously, highly empirical schemes such as the empirical soil water stress function and the supply-demand balance scheme were used as an approximation of the constraint of water transport on transpiration. Recent advances in modeling plant response to water stress further demonstrated that the empirical schemes are special cases of the mechanistic plant hydraulic models under certain conditions (Yang et al., 2023)[1]. Notably, the widely used empirical soil water stress function does not respond to VPD and hence inherently unable to capture water transport limitation in response to VPD stress.

In this study, we use a three-segment plant hydraulic model (fig. 1a) to simulate water transport in the SPAC (L. Li et al., 2021). Water transport from the soil to the root xylem and from the root xylem to the leaf is driven by water potential differences and controlled by rhizosphere and xylem conductances.

$$Q_{sx} = g_{sx}(\psi_s) \cdot (\psi_s - \psi_{rx} - h_s) \tag{2}$$

$$Q_{xl} = g_{xl}((\psi_{rx} + \psi_l)/2) \cdot (\psi_{rx} - \psi_l - h_c) \tag{3}$$

where Q_{sx} and Q_{xl} are the water flow from the soil to the root xylem and from the root xylem to the leaf, respectively; g_{sx} and g_{xl} are the respective conductances; ψ_s, ψ_{rx} and ψ_l are soil, root xylem and leaf water potentials, respectively; and h_s and h_c are soil layer depth and canopy height. In this work, instead of calculating water flow from many soil layers, we use the effective root zone depth for Midwestern crops for simplicity. We also use the average of root xylem and leaf water potentials for the calculation of xylem water potential to account for the gradual decline of water potential from the root xylem to the leaf. The rhizosphere conductance is determined by root and soil hydraulic properties, and we use a cylindrical root model (Manzoni et al., 2013) and the Brooks-Corey soil hydraulic model to calculate it:

$$g_{sx}(\psi_s) = \sqrt{RAI}/(\pi d) \cdot K_{sat} \cdot (\psi_s/\psi_{s,sat})^{-2-3/b} \tag{4}$$

[1] Yang, Y. (2023). A unified framework to reconcile theories of modeling transpiration response to drought: plant hydraulics, supply-demand balance, and empirical soil water stress. Manuscript submitted for publication.

where RAI is the root area index, d is the root zone layer depth, K_{sat} is saturated soil hydraulic conductivity, ψ_s is soil matric potential, $\psi_{s,sat}$ is saturated soil matric potential, and b is the soil particle size distribution parameter. We use a sigmoid function to parametrize xylem vulnerability curve:

$$g_{xl}(\psi_x) = g_{xl,max} \cdot (1 + (\psi_x/\psi_{x,50})^{a_1})^{-1} \tag{5}$$

where $g_{xl,max}$ is maximum xylem conductance, $\psi_{x,50}$ is the xylem water potential at 50% loss of conductance and a_1 is a shape parameter. The stomatal response function to leaf water potential is also parameterized by a sigmoid function:

$$f(\psi_l) = g_s(\psi_l)/g_{s,NHL} = (1 + (\psi_l/\psi_{l,50})^{a_2})^{-1} \tag{6}$$

where a_2 is a shape parameter, and $\psi_{l,50}$ is the leaf water potential at 50% loss of stomatal conductance compared with NHL conditions. The final stomatal conductance is the NHL conductance calculated by the coupled photosynthesis-stomatal conductance model multiplied by the stomatal response function, and the actual transpiration is

$$T = T_{NHL} \cdot f(\psi_l) \tag{7}$$

The plant hydraulic model takes soil moisture and NHL transpiration T_{NHL} as input and is solved iteratively until water flows in every segment are equal:

$$Q_{sx} = Q_{xl} = T \tag{8}$$

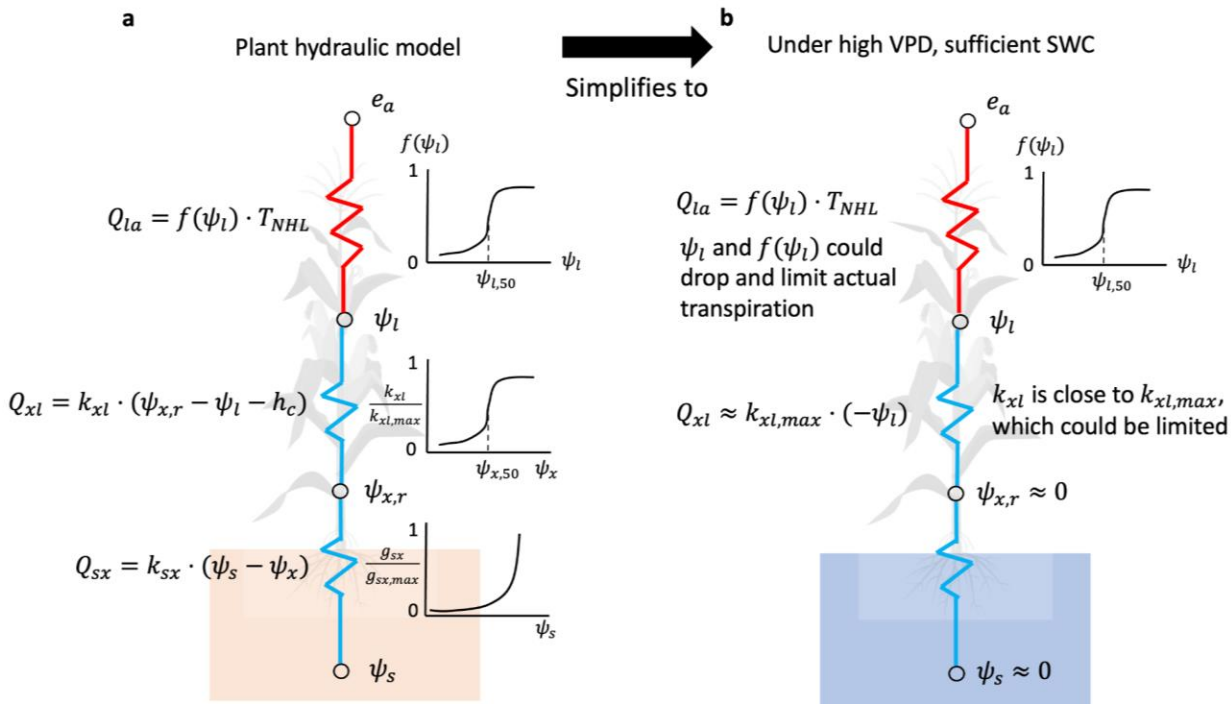

Fig. 1. Illustration of the plant hydraulic model (**a**) and how it affects plant response to VPD stress (**b**). The PHM is represented by the electric circuit analogy. On the left are the equations for water flow, and on the right are the functions for conductances. Under sufficient SWC (**b**), soil and root xylem water potentials are close to 0, and xylem conductance is close to the maximum conductance. However, leaf water potential could still drop significantly to overcome limited xylem conductance, and as a result stomatal may close in response to low leaf water potential and limit actual transpiration.

2.1.3 Radiation and turbulent transfers

We use the Noah-MP land surface model for the above-ground radiation and turbulent transfers (Niu et al., 2011; Z.-L. Yang et al., 2011). We choose Noah-MP for its wide usage in the meteorological and climate modeling communities and its computational efficiency. Readers are referred to (Niu et al., 2011; Z.-L. Yang et al., 2011) for a full description of the radiation and turbulent transfer schemes in Noah-MP. Relevant modules were extracted from the original Noah-MP model and coupled with the above-described stomatal conductance and plant hydraulic models. The full model is forced by meteorological data including air temperature, pressure, humidity, downward solar and longwave radiation, and precipitation. Because soil moisture

simulation is closely coupled with plant response to water stress (Lei et al., 2018), we use measured soil moisture as input instead of simulating it to reduce uncertainties. In the full model, the calculation of actual transpiration can be viewed as a two-step process: in the first step, the coupled photosynthesis-stomatal conductance model, together with the radiation and turbulent transfer schemes, resolves stomatal conductance and transpiration under the NHL conditions ($g_{s,NHL}$ and T_{NHL}; note, we use T to denote transpiration instead of temperature); in the second step, the plant hydraulic model takes T_{NHL} and $g_{s,NHL}$ as input and downregulates transpiration and stomatal conductance based on the water transport limitation in the SPAC and calculates the actual transpiration T and stomatal conductance g_s (see Section 4 for the implications of the two-step conceptualization). In this study, in addition to running the full model, we also conduct numerical experiments of running the plant hydraulic model only to demonstrate the limitation from plant hydraulic transport on transpiration under high VPD stress. In the plant hydraulic model only experiment, soil moisture and the NHL transpiration are prescribed and provided as input.

2.2 Demand-side Hydraulic Limitation Factor (DHLF)

Although plant hydraulic models provide the most complete mechanistic representations, they are complex, have many parameters, and, oftentimes, difficult to measure and constrain. We here derive a simplified method for simulating high VPD stress based on the plant hydraulic model. First, since we only focus on VPD stress when soil moisture is sufficient, which is typically the case for the rainfed region of the U.S. Corn Belt, the rhizosphere water transport segment can be neglected; instead, the root xylem water potential can be approximated by zero, which is close to the soil water potential when soil moisture is sufficient. The two remaining processes directly controlling transpiration response to VPD (xylem water transport and stomatal response to leaf water potential) have in total six parameters: $g_{xl,max}$, $\psi_{x,50}$, a_1, h_c, $\psi_{l,50}$, and a_2. In practice, as in many process-based physical models, many parameters could be redundant if we only focus on the final response. In this study, we only keep one parameter out of the six, the maximum xylem conductance $g_{xl,max}$, and test if only keeping the one parameter can largely reproduce the response of the original formulation. That is, we test if the effects on the final response (the

actual transpiration) of changing the other four parameters can be compensated by a corresponding change of $g_{xl,max}$. Specifically, in the test, we first do a numerical analysis similar to the plant hydraulic model only experiment mentioned in Section 2.1.3 by providing the NHL transpiration T_{NHL} as input and check if the actual transpiration response T are the same between the two formulations. We then test the two formulations using data from the flux tower (Section 2.3) to evaluate the real-world performance of the simplified formulation. We call the formulation with the only one adjustable parameter $g_{xl,max}$ to Demand-side Hydraulic Limitation Factor (DHLF), where demand-side means it only pertains to the stress from atmospheric dryness.

2.3 Study region and experiment design

We conducted the modeling experiments in seven flux tower sites located in the U.S. Corn Belt (fig. 2a and table 2). Among them, US-Ne1 (Suyker, 2016a) and US-Ne2 (Suyker, 2016b) are irrigated sites and other sites are rainfed. The meteorological forcings and soil moisture from the flux towers are used to drive the model. For the three Ne sites (US-Ne1-3), the meteorological forcings and ET data are from the FLUXNET2015 dataset (Baldocchi et al., 2001), and the soil moisture data are from the Ameriflux dataset (K. A. Novick et al., 2018). For all other sites, all measurements are from the Ameriflux dataset. For some sites (US-Br1, US-Br3, and US-Ro1) where soil moisture measurements are only available at the surface depth (e.g., 0.05 cm), we use the simulated root zone soil moisture from the full Noah-MP as a supplement (Y. Yang et al., 2021). We use site-measured LAI for the three NE sites and satellite remote sensing LAI estimates for other sites (Jiang et al., 2020; Y. Yang et al., 2021). Soil hydraulic parameters are obtained from the gSSURGO soil database (Mitter, 2017). Model parameters related to plant photosynthesis, stomatal conductance, and hydraulic transport are calibrated using the ET data from the flux towers, with values from previous literature as the baseline. Since we primarily focus on high VPD stress in this study, we calibrate and evaluate the model using midday ET observations. We only evaluate the model during the peak growing season (7/1 to 8/15 for maize and 7/15 to 9/1 for soybean) to minimize the effects caused by the uncertainties of simulated soil

evaporation. In addition, periods when model simulation indicates significant canopy or soil evaporation are also excluded.

We first run the model with no hydraulic limitation and calibrate the most important photosynthesis and stomatal conductance parameters (the maximum carboxylation rate V_{max} and g_1) to achieve good performance when VPD is low (mid-day VPD is lower than 1000 Pa). We then run the complete model with plant hydraulic components and calibrate five out of the six plant hydraulic parameters (canopy height is excluded due to its clear physical meaning; site measurement values are taken instead) related to VPD stress (rhizosphere related parameters are fixed and not calibrated). We use the parameter values from the literature (Kattge et al., 2009; Lin et al., 2015; Miner et al., 2017; Miner & Bauerle, 2019; Sperry, 2000) as the prior and only allow them to change at most 20% from their prior values during the calibration to ensure they do not deviate too much from previous research. All other parameters not included in the calibration are from previous literature or the Noah-MP look up table. The performance of the NHL model and the complete model are then compared to evaluate the importance of hydraulic limitation in simulating transpiration response to VPD stress. Finally, we evaluate the performance of the simplified DHLF formulation and compare it with the complete model with the original plant hydraulic formulation.

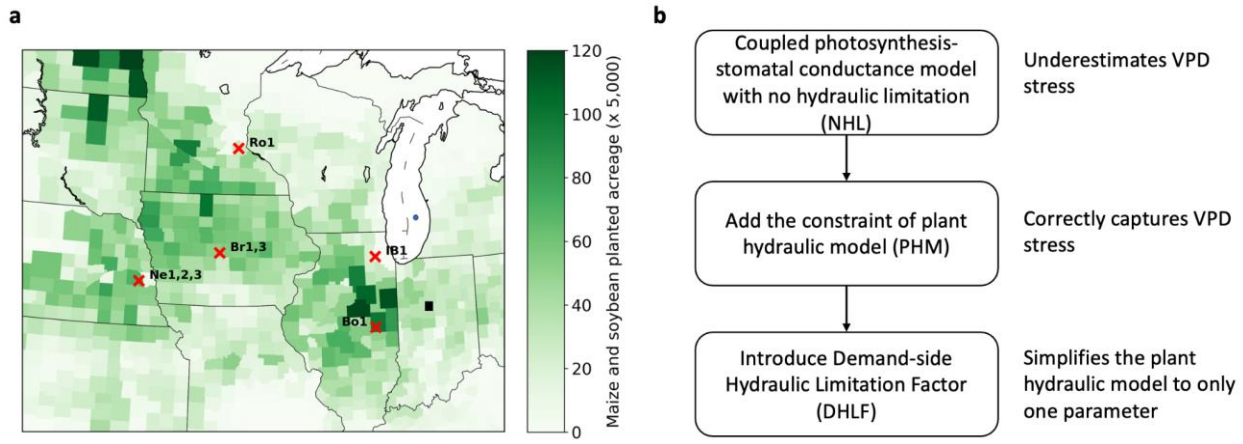

Fig. 2. The study region and flux tower sites in the U.S. Corn Belt with county level maize and soybean planted acreage in the background (**a**) and the workflow of the modeling experiments (**b**).

Table 1. The parameters calibrated in the modeling experiment. The two parameters in the NHL formulation (coupled photosynthesis-stomatal conductance only) are first calibrated under low VPD conditions. The PHM and DHLF are then calibrated with the NHL parameters fixed to the calibrated values from the first step.

NHL (first step)	**PHM (second step)**	**DHLF (second step)**
V_{max} (maximum carboxylation rate)	$g_{xl,max}$ (maximum xylem conductance)	$g_{xl,max}$ (maximum xylem conductance)
g_1 (the Medlyn stomatal conductance model slope parameter)	$\psi_{x,50}$ (xylem water potential at 50% of conductance loss)	$\psi_{x,50}$ removed (xylem conductance fixed to the maximum)
	a_1 (xylem vulnerability curve shape parameter)	a_1 removed
	$\psi_{l,50}$ (leaf water potential at 50% stomatal conductance loss due to hydraulic limitation)	$\psi_{l,50}$ fixed to $-100\ mH2O$
	a_2 (stomatal-leaf water potential response function shape parameter)	a_2 fixed to 6

Table 2. Information of the flux tower sites in the modeling experiments.

Site	**Year**	**MAP/mm**	**MAT/°C**	**Rainfed/Irrigated**	**Crop type**
US-Bo1	2000-2008	792.10	11.40	rainfed	Maize in odd years, soybean in even years
US-Br1	2005-2011	933.61	9.13	rainfed	odd maize,

					even soybean
US-IB1	2005-2011	966.76	9.52	rainfed	even maize, odd soybean
US-Ro1	2004-2012	762.45	7.71	rainfed	odd maize, even soybean
US-Br3	2005-2011	836.91	9.22	rainfed	even maize, odd soybean
US-Ne1	2003-2012	840.40	10.60	irrigated	continuous maize
US-Ne2	2003-2012	871.80	10.32	irrigated	odd maize even soybean before 2009, maize beginning 2009
US-Ne3	2003-2012	712.15	10.42	rainfed	odd maize, even soybean

3. Results

3.1 Incorporating plant hydraulic transport processes improves simulation of crop response to VPD stress

In the numerical experiment of running the plant hydraulic model only, there is significant transpiration downregulation when T_{NHL} is high even when SWC is sufficient (fig. 3). Mechanistically, high atmospheric dryness increases T_{NHL}, and if the plant xylem hydraulic conductance is limited, low leaf water potential is required to create sufficient water potential gradient to drive xylem water transport. However, low leaf water potential also causes stomata to close and limit transpiration. Note although stomatal conductance responds to high VPD negatively in the stomatal conductance model, the NHL transpiration still increases.

In the modeling experiments using flux tower data, for both maize and soybean, the NHL model significantly overestimates ET during relatively dry years compared with flux tower measurements. The overestimation mainly occurs when atmospheric dryness is high (T_{NHL} is

high) and increases when T_{NHL} increases (fig. 3). Incorporating the limitation from plant hydraulic transport largely corrects the overestimation, which indicates that stomatal conductance models alone, though also responds to VPD, are insufficient to capture high VPD stress. As indicated in the flux tower measured data, root zone soil moisture in these corn belt sites rarely drops below 0.25, even in an extreme drought year like 2012; as a result, soil moisture is not a significant limiting factor for crop transpiration (fig. S1). In fact, even in the extreme drought year of 2012 where soil moisture stress does play a role, high VPD stress is still the dominant stress factor. Detailed time series analysis (fig. 4) reveals that the NHL transpiration has the largest overestimation compared to flux tower observation when VPD is high; during the entire peak growing season, soil moisture at 0.25 m depth, which covers the upper fraction of the root zone, is almost always above 0.25.

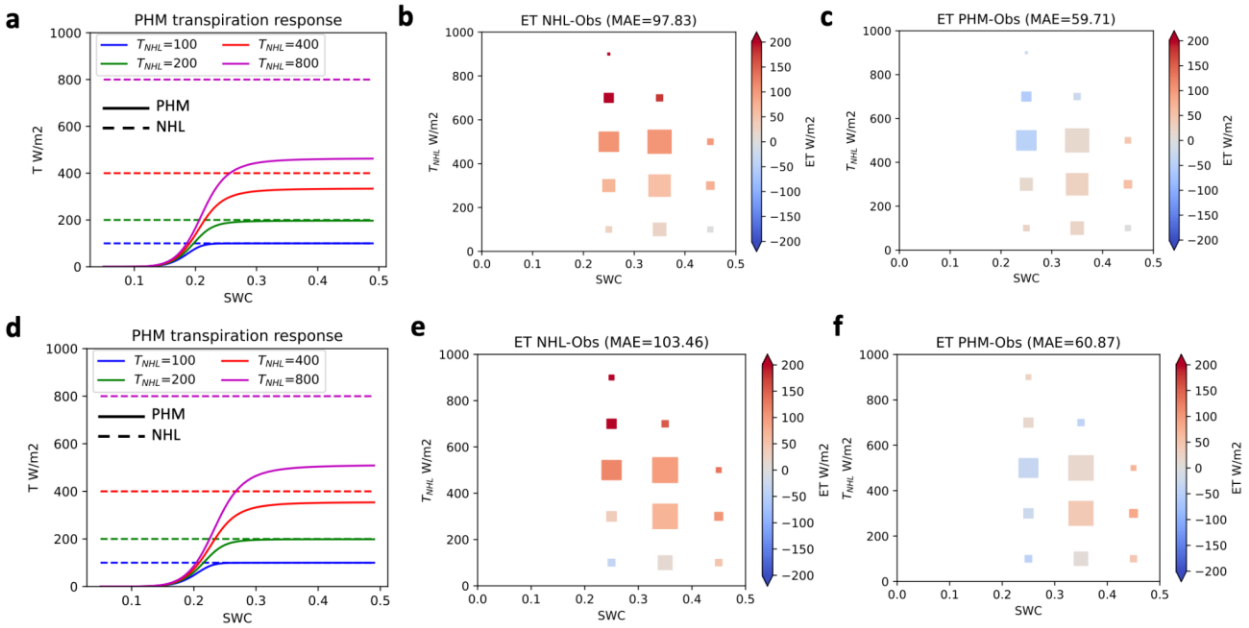

Fig. 3. **a,** The numerical experiments of the transpiration responses; the dashed horizontal lines are the NHL transpiration (NHL does not respond to soil water stress and underestimate VPD stress) and the solid lines are the transpiration response of the PHM. **b**, The bias of the simulated ET by models without hydraulic limitation; and **c,** with plant hydraulic processes evaluated with flux tower data for maize. The joint distribution of T_{NHL} and SWC is binned, and the square size represents the density of data in the binned region. Mean absolute errors (MAE) are given in the figure title. **d-f**, The same as **a-c** but for soybean.

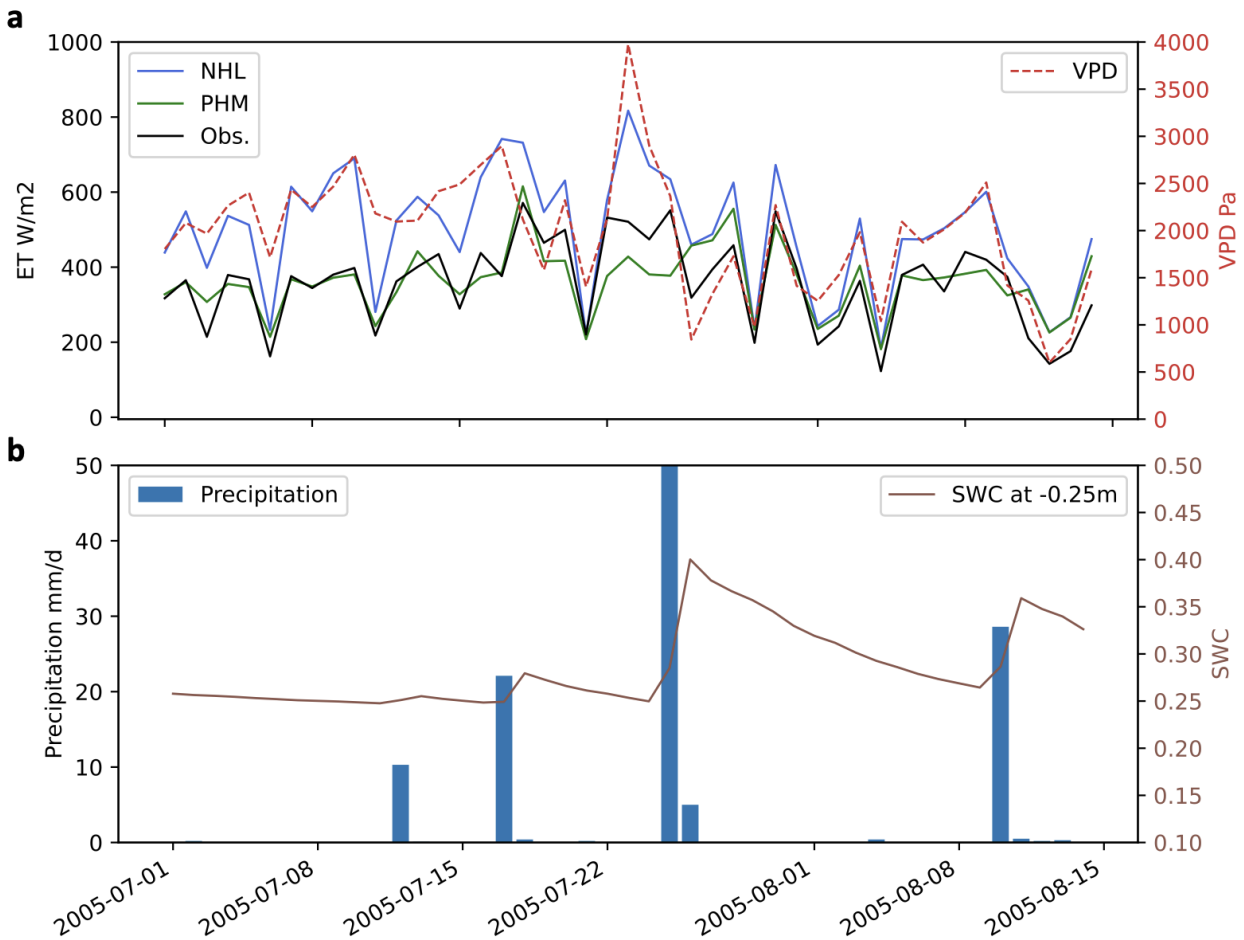

Fig. 4. **a**, Time series of ET calculated with (PHM) and without (NHL) hydraulic transport limitation (NHL) compared with flux tower observed data (Obs.) for US-Ne3 in 2005; VPD is also shown. **b**, time series of precipitation and SWC at 0.25 m depth for the same period.

3.2 The effectiveness and efficiency of Demand-side Hydraulic Limitation Factor

In the numerical analysis, the DHLF formulation achieves nearly identical response as the original plant hydraulic model across realistic ranges of T_{NHL} (from 0 to 1000 W/m^2) and the six plant hydraulic parameters (fig. 5 and fig. S2). The effects on the actual transpiration response of changes in other parameters can be compensated by an appropriate change of $g_{xl,max}$ alone in the DHLF formulation. This indicates that the six parameters related to VPD stress in the original PHM are largely redundant in terms of calculating the final response of actual

transpiration and the simplified DHLF formulation is effective and more efficient. Specifically, DHLF captures the effects of changing h_c and $\psi_{l,50}$ accurately, showing little difference between the two formulations. $\psi_{l,50}$ and h_c are also the most important parameters in addition to $g_{xl,max}$, which is preserved by DHLF. There are slight differences between DHLF and the original PHM when $\psi_{x,50}$, a_1, or a_2 are modified; however, the three parameters are relatively insignificant for capturing VPD response, and the two shape parameters are inherently empirical, and thus the differences can be considered minor.

Modeling experiments using flux tower data confirms the effectiveness of the DHLF formulation. The calibrated DHLF and original PHM have similar performance evaluated against flux tower ET observation (fig. 6**abde**). The responses between the two formulations are also similar if compared against each other (fig. 6**cf**); the minor differences between them are mainly caused by the presence of the response to soil moisture stress in the PHM, which is insignificant in the study region. A typical time series similar to fig. 4 is provided in fig. S3.

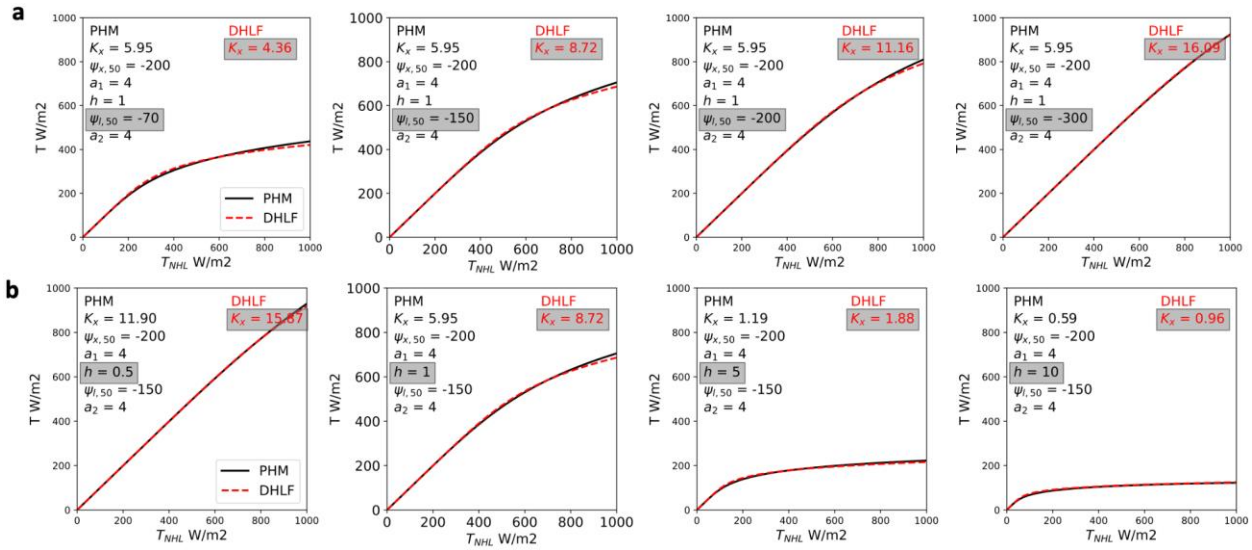

Fig. 5. The actual transpiration response of the DHLF formulation compared with the original PHM under sufficient SWC with T_{NHL} prescribed as input. **a**, change $\psi_{l,50}$ in the PHM and calibrate the only parameter ($g_{xl,max}$) in DHLF to match the response of PHM. **b**, change h_c in the PHM and calibrate DHLF to match the response. The parameters on the left are from the PHM (gray background denotes the parameter changed), and the parameter on the right is the

DHLF formulation. The solid black lines (PHM) and dashed red lines (DHLF) largely overlap. For changes of other parameters in the PHM, please see fig. S2.

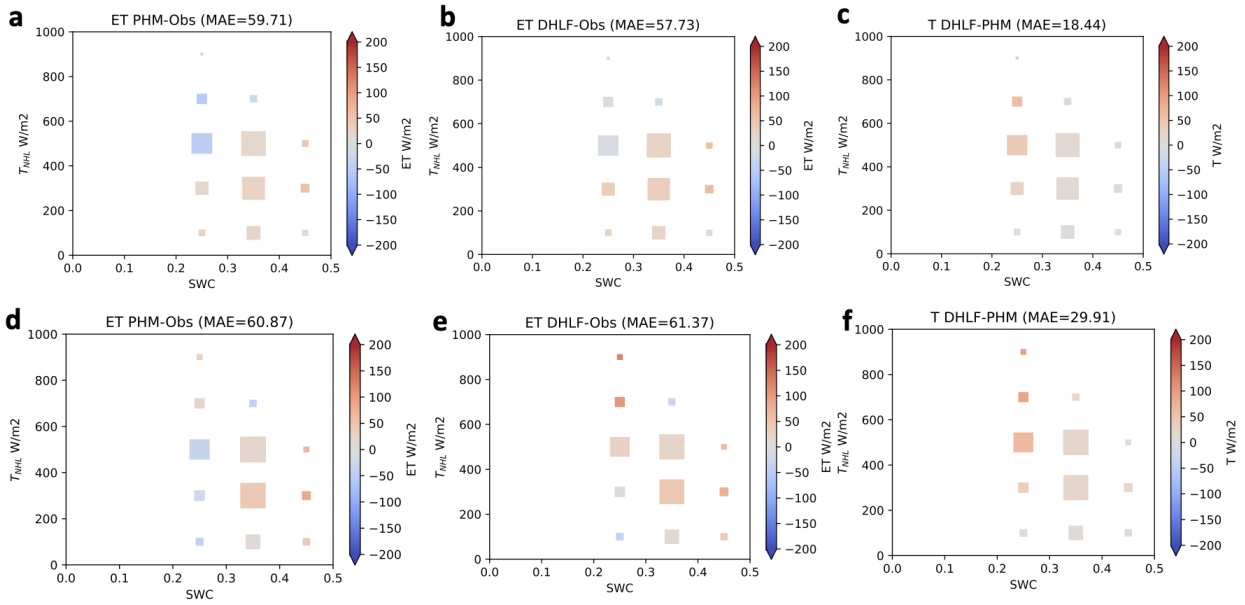

Fig. 6. The bias of the simulated ET by the original PHM (**a**) and the DHLF formulation (**b**) evaluated with flux tower data, and the bias of the simulated transpiration by the DHLF formulation evaluated against the original PHM for maize (**c**). The figure layout is the same as in fig. 6**bcef**. **d-f**, the same as **a-c** but for soybean.

4. Discussion

Our modeling experiments demonstrate that plant hydraulic processes are important in capturing high VPD stress in the U.S. Corn Belt. In the experiments, the NHL model configuration with the coupled photosynthesis-stomatal conductance model alone severely overestimates crop transpiration (underestimate VPD stress) under high VPD and incorporating plant hydraulic transport processes significantly improves the simulation of transpiration. Previous studies have shown that theoretically PHM accentuates the effect of VPD stress on transpiration regardless of soil water status (Liu et al., 2020). Our study indicates that in regions where VPD stress is high such as the Midwestern U.S., the widely used stomatal conductance model alone is insufficient for capturing VPD stress, and thus the representation of plant hydraulics is necessary. Notably,

as some empirical schemes to represent water transport limitations, such as the empirical soil water stress function (Feddes et al., 1976), do not respond to VPD, many land surface models configured with these schemes will also be insufficient for capturing VPD stress. Therefore, we argue that plant hydraulics would be beneficial to correctly simulating crop response to rising VPD especially under future climate scenarios.

Our study also demonstrates that the PHM can be largely simplified for simulating transpiration response to VPD stress. One major downside of PHM preventing its wide adoption is its complexity and the large number of parameters. We here demonstrate that, specifically for the response to VPD stress, the parameter space can be compressed with little to no sacrifice of accuracy. The six parameters involved in the response to VPD stress can be simplified to one parameter. Numerical model experiments show that the effects of changing other parameters can be achieved by an appropriate change of the DHLF. Flux tower site testing further demonstrates that the performance of the simplified DHLF formulation is similar to the original PHM in terms of capturing the response to VPD stress. We envision that the DHLF method can be a useful tool in improving the simulation of plant response to VPD stress in many cases where 1) the final response is the main point of interest instead of detailed process understanding, 2) data availability is limited, and therefore model parsimony is preferred.

Note that a few limitations exist in this analysis. First, there are two prerequisites to the conclusion that the coupled photosynthesis-stomatal conductance alone is insufficient for capturing high VPD stress in the U.S. Corn Belt: (1) the NHL model alone with parameters close to literature values underestimates high VPD stress, and (2) the NHL model structure and literature values of its parameters are largely correct. The second one is indispensable because with the flux tower data only (atmospheric forcing and evapotranspiration measurements), the coupled photosynthesis-stomatal conductance model alone can for certain match the flux tower data with appropriate functional form and parameters (even if the widely used Medlyn or Ball-Berry models cannot, a new functional form can be developed to match the data). To support the conclusion without (2), more measurement data or experiments will be required, e.g., sap flow, leaf water status. Second, the two-step formulation of sequentially running the NHL model and

the PHM is only one way of setting up a land surface model with plant hydraulic processes. We choose this two-step formulation for its simplicity and ease of use, and we do not expect it to significantly interfere with the main points of this study. The first point regarding the inadequacy of the coupled photosynthesis-stomatal conductance for capturing VPD stress does not depend on how the PHM is incorporated in the full model. For the second point regarding the redundancy of PHM parameters, we do expect the exact results to be slightly different if a different coupling method is used for the PHM, but we still expect the effect of hydraulic constraint on transpiration to be similar on a first-order basis, and most importantly there is still sufficient room for simplification.

5. Conclusion

In this study, through numerical experiments and site testing, we demonstrate that the widely used coupled photosynthesis-stomatal conductance model alone is insufficient for simulating crop transpiration response to VPD stress in the U.S. Corn Belt. Plant hydraulic transport processes are required for correctly capturing crop response to VPD stress even under sufficient soil moisture. We then introduce a simplified DHLF formulation derived from the plant hydraulic model with only one parameter specifically for simulating the limitation of hydraulic transport on transpiration. The simplified formulation achieves nearly the same response as the original PHM and similar performance in flux tower site testing. We envision that the improved understanding of the role that plant hydraulics plays in crop response to VPD and the simplified modeling method would facilitate future research and applications in the management and adaptation of agricultural ecosystems to a changing climate.

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Open Research

The data that support the findings of this study are available in Ameriflux at https://ameriflux.lbl.gov/ and other literature referenced in the manuscript. The code for producing the analysis is available on Github via Zenodo (Frostbite7. (2023). Frostbite7/crop_hydro: Preview version for investigating VPD stress on crops (preview). Zenodo. https://doi.org/10.5281/zenodo.8432287).

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