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Key Points:

- Coupled photosynthesis-stomatal conductance models alone underestimate vapor pressure deficit (VPD) stress effects on crop stomatal conductance and transpiration
- Limited plant hydraulic transport capability could play a role in plant response to high VPD
- A simplified representation of plant hydraulic model for capturing VPD stress on plants is proposed

Supporting Information:

Supporting Information may be found in the online version of this article.

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Explicit Consideration of Plant Xylem Hydraulic Transport Improves the Simulation of Crop Response to Atmospheric Dryness in the U.S. 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 VPD constraints in the widely used coupled photosynthesis-stomatal conductance models alone are inadequate to fully capture VPD stress effects. 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; K. 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.

In modern land surface models, a coupled photosynthesis-stomatal conductance model (Ball et al., 1987; Leuning, 1995; Medlyn et al., 2011) combined with a dedicated 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 accounting for hydraulic transport 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). The stomatal conductance model is relatively well constrained thanks to a large number of prior studies and established parameter data sets (Buckley, 2017; Damour et al., 2010; Lin et al., 2015; Miner et al., 2017). However, accurately representing the dedicated scheme accounting for hydraulic transport 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). Note, following previous similar research (Sloan et al., 2021), we here use "beta" or "the beta function" to specifically refer to the empirical soil water stress function, though many other schemes like the plant hydraulics models may also name the stress factor based on leaf water potential (or other plant hydraulic variables) as "beta." Also note that the beta function does not simulate any hydraulic transport from the soil through the plant root and xylem to the leaves, but it plays the same role and is an extreme simplification of the PHM (Sloan et al., 2021). Therefore, it is in the category of plant hydraulic transport modules.

A widely spread pre-conception is that the stomatal conductance module resolves stomatal response to light, temperature, VPD, and other atmospheric variables, while the plant hydraulic transport module, be it empirical or mechanistic, resolves the effects of soil water stress. Sometimes, "hydraulic limitation" or "hydraulic transport limitation" are even specifically associated with the limitation caused by insufficient soil water. However, that pre-conception has been increasingly challenged by research in the past two decades (Anderegg & Venturas, 2020; Detto & Pacala, 2022; Grossiord et al., 2020; Hubbard et al., 2001; Liu et al., 2020; Oren et al., 1999; Paschalis et al., 2023). These studies demonstrated that although the coupled-photosynthesis stomatal conductance model already considers the constraint of VPD on stomata, plant hydraulic transport imposes additional limitations on stomatal conductance under high VPD conditions with or without soil water limitation (Grossiord et al., 2020; Hubbard et al., 2001; Liu et al., 2020; Oren et al., 1999). In other words, VPD stress captured by the stomatal conductance model only could be insufficient. Notably, a recent study highlighted that PHMs accentuate the effect of VPD stress across global ecosystems (Liu et al., 2020), underlining the necessity of PHMs to accurately capture the full effects of VPD stress on leaf gas exchange.

Meanwhile, the widely used empirical soil water stress function in current-generation and previous-generation 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. 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. Besides its importance for regional economics and food production, we choose the U.S. Corn Belt as the study region also because it has a relatively humid climate and usually sufficient soil moisture but periodically suffers from high VPD stress (Kimm et al., 2020). Therefore, it is an important and appropriate region to test if plant hydraulic processes are important even without soil water stress. Specifically, we ask two questions: (a) To what extent are plant hydraulic processes important in capturing VPD stress in the U.S. Corn Belt? (b) 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; We then conduct modeling experiments in flux tower sites in the U.S. Corn Belt 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, especially considering the increasing VPD as a robust climate change projection for this study region and beyond (IPCC Climate Change, 2013; K. A. Novick et al., 2024).

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

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

where $g_{s,\mathrm{NHL}}$ 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 CO$_2$ assimilation rate (μmol m^{-2} s^{-1}), and C_a is atmospheric CO$_2$ 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. Lastly, with the $g_{s,\mathrm{NHL}}$, we can calculate the transpiration without hydraulic limitation T_NHL. If neglecting boundary layer resistance,

$$T_\mathrm{NHL} \approx g_{s,\mathrm{NHL}} \cdot \mathrm{VPD} \tag{2}$$

In general, leaf boundary layer and atmospheric boundary layer cannot be neglected, and we use a land surface model to resolve those boundary layer processes (Section 2.1.3). One thing to note is that in the presence of water stress, stomatal resistance tends to dominate the two boundary layer resistances; therefore, neglecting boundary layer resistance should be a close approximation in the stress scenarios.

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 (Figure 1b). Many current-generation land surface models use process-based PHM 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 PHM under certain conditions (Sloan et al., 2021). 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 (Figure 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 conductance.

$$Q_{sx} = g_{sx}(\psi_s)\cdot(\psi_s - \psi_{rx} - h_s) \tag{3}$$

$$Q_{xl} = g_{xl}((\psi_{rx} + \psi_l)/2)\cdot(\psi_{rx} - \psi_l - h_c) \tag{4}$$

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

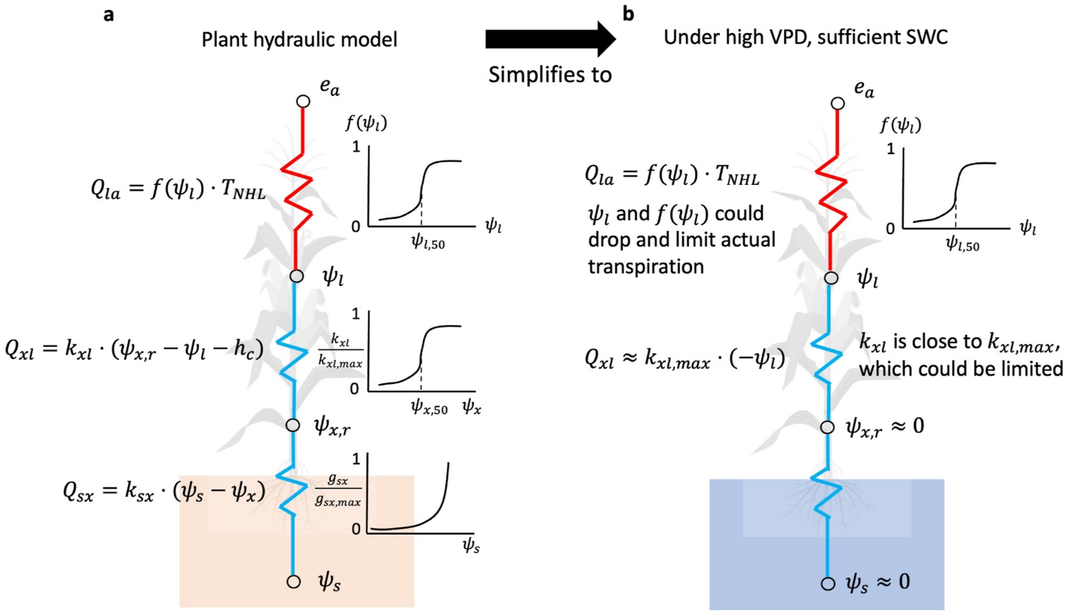

Figure 1. Illustration of the plant hydraulic model (a) and how it affects plant response to vapor pressure deficit stress (b). The plant hydraulic models is represented by the electric circuit analogy. On the left are the equations for water flow, and on the right are the functions for conductance. 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.

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:

$$g_{sx}(\psi_s) = \sqrt{\mathrm{RAI}}/(\pi d)\cdot K_{\mathrm{sat}}\cdot\left(\psi_s/\psi_{s,\mathrm{sat}}\right)^{-2-3/b} \tag{5}$$

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, $\psi_{s,\mathrm{sat}}$ is saturated soil matric potential, and b is the soil particle size distribution parameter. We use a sigmoid function to parametrize xylem vulnerability curve:

$$g_{xl}(\psi_x) = g_{xl,\max}\cdot\left(1+\left(\psi_x/\psi_{x,50}\right)^{a1}\right)^{-1} \tag{6}$$

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:

$$f(\psi_l) = g_s(\psi_l)/g_{s,\mathrm{NHL}} = \left(1+\left(\psi_l/\psi_{l,50}\right)^{a_2}\right)^{-1} \tag{7}$$

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 if neglecting boundary layer resistance in the water stress conditions, the actual transpiration is

$$T \approx T_{\mathrm{NHL}}\cdot f(\psi_l) \tag{8}$$

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:

$$Q_{sx} = Q_{xl} = T \tag{9}$$

Though VPD does not directly appear in any of the equations of the PHM, the transpiration without hydraulic limitation, T_{NHL}, incorporates the effects of VPD. T_{NHL}, calculated by the stomatal conductance model alone described in Section 2.1.1 (Equation 2), is primarily determined by atmospheric conditions like light, temperature, and VPD. When VPD is high, T_{NHL} could be high. To sustain the high transpiration demand, the root xylem to leaf water flow, Q_{xl}, also needs to be high. However, the xylem conductance as calculated by Equation 6 could be limited, in which case, leaf water potential ψ_l has to drop substantially to create a sufficient water potential gradient for the high xylem water flow. As a result of leaf water potential drop, stomatal could close, and the actual transpiration will decline to reach the equilibrium. This is the mechanism how plant hydraulics could play a role in the stomatal response to VPD stress. Notably, this could happen even under sufficient soil moisture. When soil moisture is high, xylem water potential is usually also high because water transport from the soil to the root is easy, and as result, xylem conductance is close to its maximum value $g_{xl,\max}$. However, the maximum xylem conductance could still be limited for some species, and therefore hydraulic limitation could still occur when VPD is high. Note, although the effect of VPD causing stomatal closure is already partially captured by the stomatal conductance model described in Section 2.1.1 (e.g., the VPD term in the Medlyn stomatal model), this study is to specifically investigate the additional constraint posed by plant hydraulic transport in response to VPD stress (for crops) as described above and suggested by studies (Anderegg & Venturas, 2020; Detto & Pacala, 2022; Liu et al., 2020; Paschalis et al., 2023).

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 PHM. 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 ($g_{s,\mathrm{NHL}}$ 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 $g_{s,\mathrm{NHL}}$ 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 an iterative way. The first step can be viewed as the default Noah-MP model without any hydraulic transport limitation, equivalent to fixing the beta function in the original Noah-MP to 1. The second step can be viewed as replacing the beta function in the original Noah-MP with a PHM, similar to a previous study (L. Li et al., 2021), except that Li et al. (2021) used a more complex PHM considering capacitance and applied the stress factor to other variables while we apply the stress factor directly to stomatal conductance. 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 inputs.

2.2. Demand-Side Hydraulic Limitation Factor (DHLF)

Although PHM 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

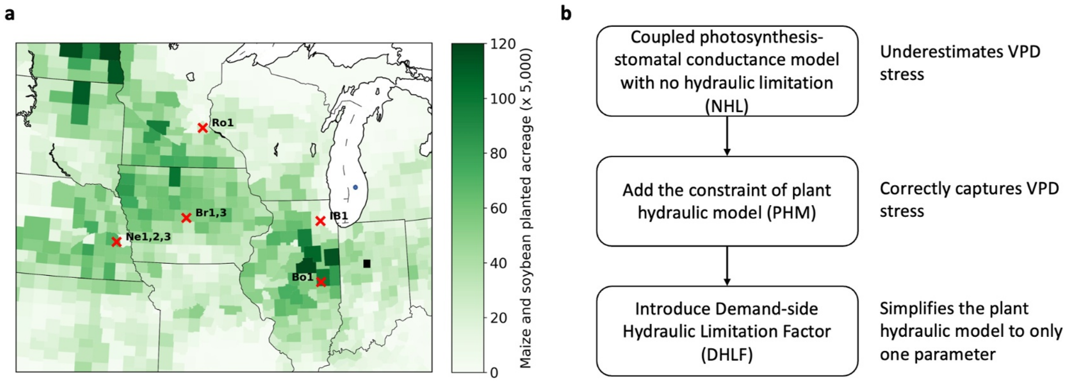

Figure 2. The study region and flux tower sites in the U.S. Corn Belt with county level maize and soybean planted acreage in the background (a) and the workflow of the modeling experiments (b).

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 five 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 eight flux tower sites located in the U.S. Corn Belt (Figure 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 data set (Baldocchi et al., 2001), and the soil moisture data are from the Ameriflux data set (K. A. Novick et al., 2018). For

Table 1
The Parameters Calibrated in the Modeling Experiment

NHL (first step)	PHM (second step)	DHLF (second step)
$V_{\max}$ (Maximum carboxylation rate)	$g_{\text{xl,max}}$ (Maximum xylem conductance)	$g_{\text{xl,max}}$ (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

Note. 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.

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

all other sites, all measurements are from the Ameriflux data set. 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 leaf area index (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 (7/1–8/15 for maize and 7/15–9/1 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 NHL 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 (midday VPD is lower than 1,000 Pa). We use the SCE-UA approach (Duan et al., 1992) for parameter calibration similar to a previous study (Y. Yang et al., 2021). 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 & Bauerle, 2019; Miner et al., 2017; 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 (Table 1 and Table S1 in Supporting Information S1). 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.

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 (Figure 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 (Figure 3).

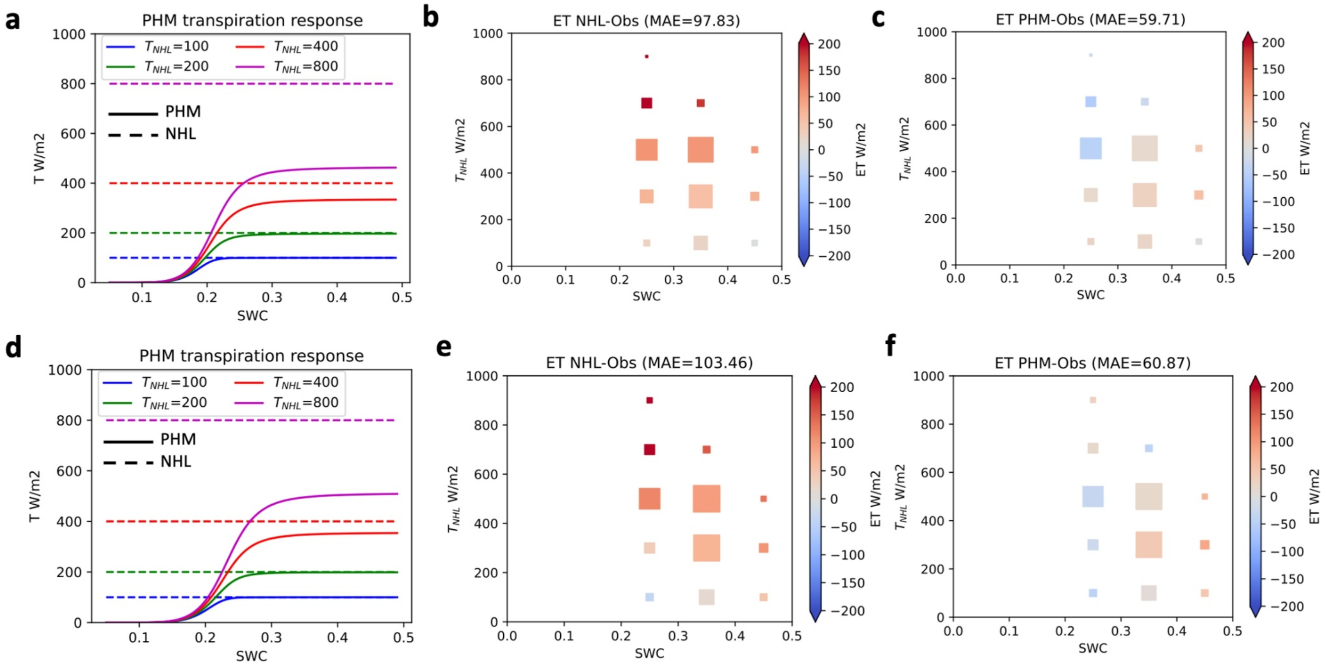

Figure 3. The response differences and the error comparisons between no hydraulic limitation (NHL) and plant hydraulic models (PHM) across eight flux tower sites. (a) The numerical experiments of the transpiration responses (using the prior hydraulic parameters for the two crops); the dashed horizontal lines are the NHL transpiration (NHL does not respond to soil water stress and underestimate vapor pressure deficit 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.

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 (Figure S1 in Supporting Information 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 (Figure 4 and Figure S4 in Supporting Information S1) reveals that the NHL transpiration has the largest overestimation compared to flux tower observation when VPD is high.

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 1,000 W/m^2) and the six plant hydraulic parameters (Figure 5 and Figure S2 in Supporting Information S1). 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 (Figures 6a, 6b, 6d and 6e). The responses between the two formulations are also similar if compared against each other (Figures 6c and 6f); the minor differences between them are mainly caused by the presence of the response to soil

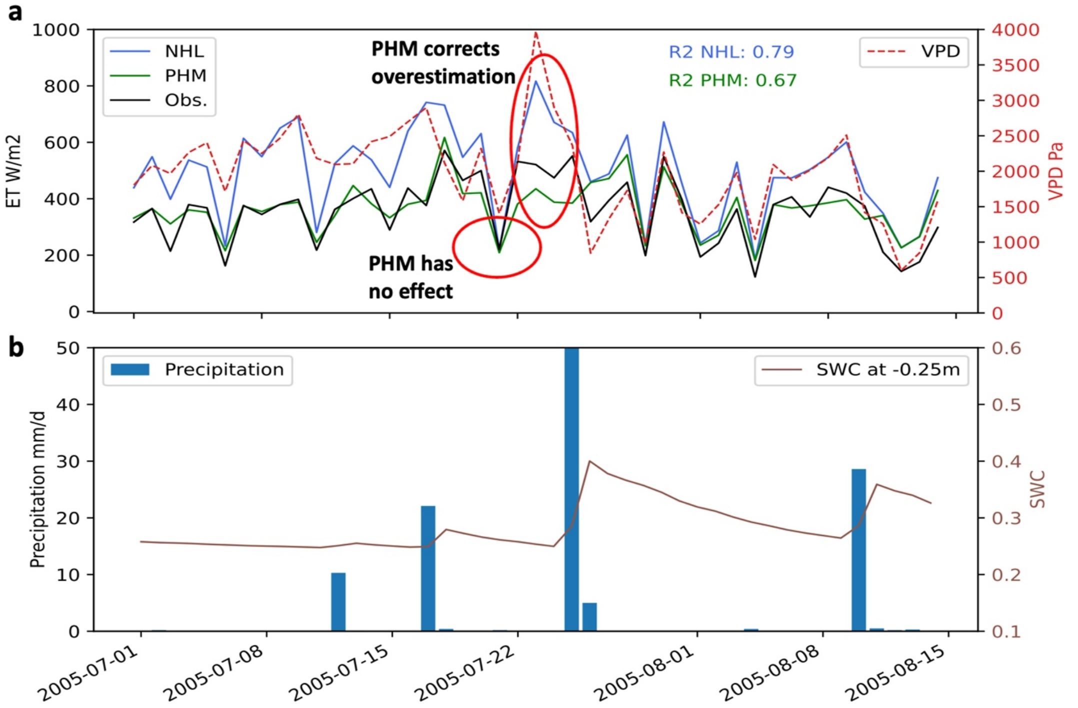

Figure 4. (a) Time series of ET calculated with (plant hydraulic models (PHM)) and without (no hydraulic limitation (NHL)) hydraulic transport limitation (NHL) compared with flux tower observed data (Obs.) for US-Ne3 in 2005; vapor pressure deficit VPD is also shown. (b) Time series of precipitation and SWC at 0.25 m depth for the same period. Note the two red circles in a show that PHM corrects the overestimation of NHL when VPD is high, yet has less effect when VPD is low. Thus, PHM is not a universal magnitude correction; it also improves the temporal dynamics, as indicated by the improvement in R^2.

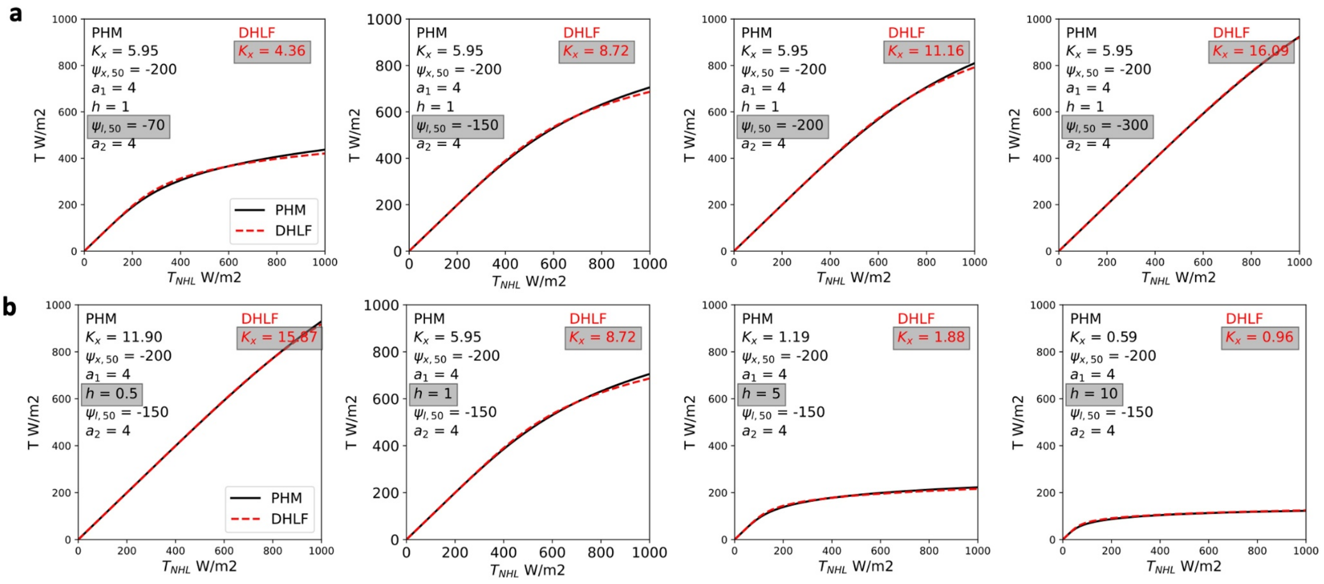

Figure 5. The actual transpiration response of the Demand-side Hydraulic Limitation Factor (DHLF) formulation compared with the original plant hydraulic models (PHM) under sufficient SWC with T_{NHL} prescribed as input. (a) Change $\psi_{l,50}$ in the PHM and calibrate the only parameter ($g_{\mathrm{xl,max}}$) 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 Figure S2 in Supporting Information S1.

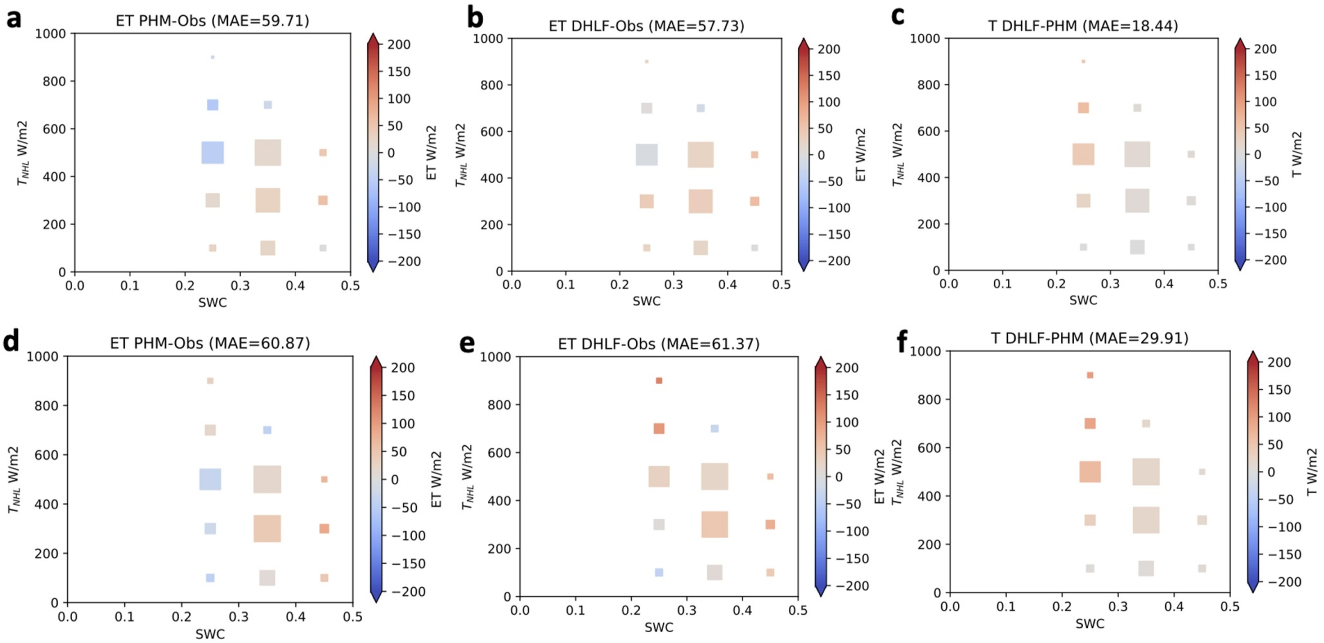

Figure 6. The bias of the simulated ET by the original plant hydraulic models (PHM) (a) and the Demand-side Hydraulic Limitation Factor (DHLF) formulation (b) evaluated with flux tower data, and the bias of the simulated transpiration by the DHLF formulation evaluated against the original PHM for maize (c). The figure layout is the same as in panels, b, c, e and f. (d–f) The same as (a–c) but for soybean.

moisture stress in the PHM, which is insignificant in the study region. A typical time series similar to Figure 4 is provided in Figure S3 of Supporting Information S1.

4. Discussion

4.1. The Importance of Incorporating Plant Hydraulic Transport in Crop Response to VPD Stress

Our modeling experiments demonstrate that plant hydraulic processes are important in capturing high VPD stress in the U.S. Corn Belt even under relatively sufficient soil moisture. 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 VPD constraints in the widely used stomatal conductance model alone are inadequate to fully capture VPD stress effects, 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.

4.2. The Utility of the Simplified Hydraulic Formulation

Our study also demonstrates that the PHM can be largely simplified for simulating transpiration response to VPD stress in the absence of soil water 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. In our DHLF formulation, we choose to keep the maximum xylem hydraulic conductance $g_{xl,\max}$ out of the six relevant parameters for its high impact, that is, the PHM response is highly sensitive to it. Two of the other parameters, leaf water potential at half stomatal closure $\psi_{l,50}$ and canopy height h, are also highly sensitive, so they could be used in the DHLF as well depending on the researchers' preference. One thing to note is that the one parameter chosen for the DHLF formulation no longer carries its original physical meaning; instead, it is a proxy for the total effects of all six parameters. The remaining parameters, especially the shape parameters, are relatively insignificant; the response differences caused by different values of the shape parameters (within a reasonable range) are relatively minor or can be partially compensated by the more important parameter kept in the DHLF formulation. However, due to their insignificant effects, the effects of changing other more important parameters cannot be compensated by the shape parameters. Therefore, those shape parameters cannot be the one kept in the DHLF formulation. 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 (a) the final response is the main point of interest instead of detailed process understanding, (b) data availability is limited, and therefore model parsimony is preferred.

4.3. Limitations and Future Work

There are a few limitations 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: (a) the NHL model alone with parameters close to literature values underestimates high VPD stress, and (b) 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 (c), more measurement data or experiments will be required, for example, sap flow, leaf water status (Oren et al., 1999; Sperry, 2000). 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 two 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.

Another important area that should receive more attention in future work is the interaction between water and carbon. In our study, we focus on transpiration response to VPD stress; carbon assimilation is implicitly linked to water use through stomatal conductance (an example time series is provided in Figure S5 of Supporting Information S1). However, there are other mechanisms by which water stress can affect carbon assimilation (J. Flexas & Medrano, 2002; J. Flexas et al., 2012; Zhou et al., 2013). Prior studies have established that, in addition to stomatal effects, water stress can cause photosynthetic capacity to decline (J. Flexas & Medrano, 2002; J. Flexas et al., 2004; Zhou et al., 2013). Some studies reported that non-stomatal effects are insignificant under mild stress, but become more important under severe stress (Tombesi et al., 2015). Moreover, over longer time scales, water stress can affect plant growth and development through phenology and carbon allocation (Chaves et al., 2002; Oliveira et al., 2021; Reich & Borchert, 1984). These effects are especially important for annual plants like crops because their structures can change in a relatively short period of time. In some cases, soil water deficit may not limit transpiration instantaneously, but could stimulate plants to allocate more carbon to the roots, affecting long term growth (Sharp & LeNoble, 2002; Xu et al., 2013). In summary, how carbon assimilation responds to water stress has more complex mechanisms compared to transpiration, and those mechanisms are even relatively less understood. In many land surface models including the plant hydraulic version of Noah-MP (L. Li et al., 2021) and CLM5 (Kennedy et al., 2019), an empirical scaling factor based on plant hydraulic variables is applied to the plant photosynthetic capacity to account for the non-stomatal effects of water stress on carbon assimilation. However, we do not have the same confidence in its underlying mechanisms compared with transpiration. For example, how much do the diffusive limitation (stomatal effects) and the metabolic limitation (non-stomatal effects) play a role? When does each of them play a dominant role? Significantly more work is required to better connect the process understanding and modeling methods for carbon assimilation response to water stress.

Therefore, we choose to focus on transpiration in this paper and propose that future research can build on the improved understanding of stomatal and transpiration response to water stress to improve understanding water-carbon interactions. Namely, future research should more explicitly investigate how each of the stomatal and non-stomatal factors affect carbon assimilation response to water stress and establish a more mechanistic based and trustworthy modeling strategy.

5. Conclusion

In this study, through numerical experiments and site testing, we demonstrate the VPD constraints in the widely used coupled photosynthesis-stomatal conductance models alone are inadequate to fully capture VPD stress effects on stomatal conductance and transpiration 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.

Data Availability Statement

The data that support the findings of this study are available in Ameriflux at https://ameriflux.lbl.gov/data/download-data/ (register an account and select the eight sites in Table 2 to download) and other literature referenced in the manuscript (Kattge et al., 2009; Lin et al., 2015; Miner & Bauerle, 2019; Miner et al., 2017; Sperry, 2000). The code for producing the analysis is available on Github via Zenodo (Y. Yang, 2024).

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