

## Commentary

# Plant hydraulics play a critical role in Earth system fluxes

Stomatal pores on leaves mediate major terrestrial water and carbon fluxes. Thus, understanding and modeling of stomatal behavior is crucial for predicting climate change impacts on ecosystems, agricultural yields, and biosphere–atmosphere feedbacks. Terrestrial biosphere models have long used empirical (i.e. statistical) models of simulating stomatal conductance and how it responds to the environment (Fig. 1). While such an approach has some advantages, it has numerous drawbacks, particularly well documented poor performance during drought conditions and large uncertainty in future and out-of-sample predictions (Powell *et al.*, 2013; Trugman *et al.*, 2018). Two recent studies published in this issue of *New Phytologist* – Eller *et al.* (2020; pp. 1622–1637) and Sabot *et al.* (2020; pp. 1638–1655) – present exciting advances for the field because they incorporate physiology of plant water (hydraulic) transport into biosphere models and link water transport to stomatal conductance via evolutionary optimization theories. Together, these approaches go a long way towards overcoming some long-standing limitations in the field and open up fascinating new research avenues.

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*‘... this increase in complexity from hydraulic transport and hydraulic-based stomatal optimizations is useful, justified, and powerful...’*

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The fundamental physiology of plant hydraulics has been understood for a long time. Based on gradients in water potential, plants take up water from the soil, transport this water to leaves via the cohesion–tension theory, and lose water to the atmosphere through stomata. During drought, the water potential declines in the hydraulic continuum until at species-specific thresholds embolisms enter xylem conduits and impair water transport. Key functional traits needed to describe the hydraulic continuum and its vulnerability to stress include the hydraulic conductance of tissues, the area of roots, sapwood, and leaves, and the vulnerability of tissues to embolism, often termed the ‘vulnerability curve’ (Fig. 1). A broad body of ecophysiological literature has quantified many of these key plant hydraulic traits, particularly vulnerability curves, across species, environments, and life-stages. Thus, plant

hydraulics mechanistically links soil and atmospheric water stress to leaf gas exchange and also provides a clear and internally-consistent evolutionary optimization – plants are expected to maximize fitness by maximizing the benefits of carbon uptake minus the risks of hydraulic damage (Wolf *et al.*, 2016; Sperry *et al.*, 2017).

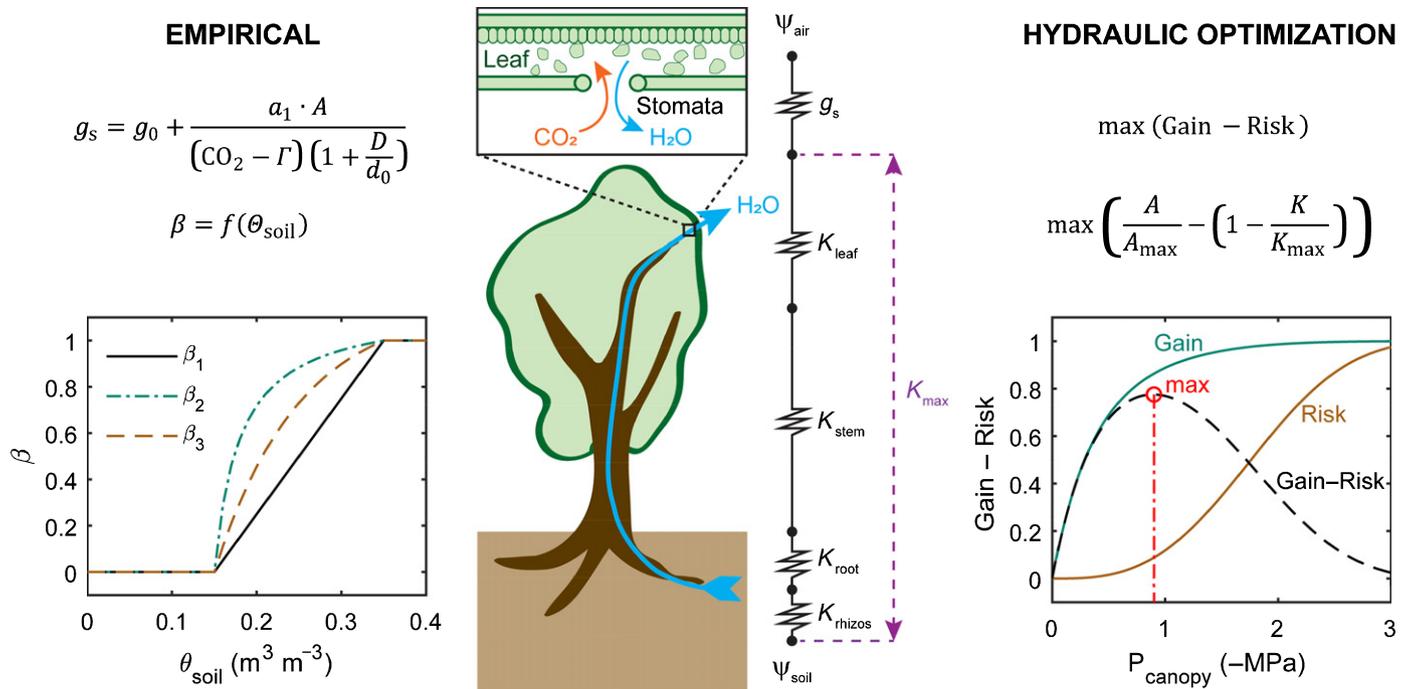
Most current and previous biosphere models use empirical relationships between stomatal conductance and photosynthesis, vapor pressure deficit (VPD), and carbon dioxide (CO<sub>2</sub>) concentrations with an additional ‘scaling’ soil moisture stress function, often termed ‘ $\beta$ ’ (Fig. 1). While these functional responses of stomata are widely observed, this formulation comprises a combination of an empirical model and a ‘black-box’ approach for the  $\beta$ -function. Critically, this approach lacks rigorous plant physiology and the  $\beta$ -function has been shown to have large carbon cycle impacts (Trugman *et al.*, 2018). Several biosphere models have incorporated plant hydraulic transport (Hickler *et al.*, 2006; Bonan *et al.*, 2014; Xu *et al.*, 2016; Kennedy *et al.*, 2019), which is a useful step, but these efforts did not link hydraulic transport to stomatal conductance with optimizations based on hydraulic risks and were not broadly tested across many biomes and sites. Furthermore, previous optimization theories were not ideal for linking water transport to stomatal conductance because they did not include hydraulic damage as one of the important risks of opening stomata. Recent hydraulic-based optimization theories have shown powerful improvements at the leaf and plant level and have opened the door for tests in biosphere models (Wolf *et al.*, 2016; Sperry *et al.*, 2017; Anderegg *et al.*, 2018b; Eller *et al.*, 2018; Venturas *et al.*, 2018).

Eller *et al.* (2020) and Sabot *et al.* (2020) implement slightly different versions of a hydraulic-based stomatal optimization put forward by Wolf *et al.* (2016) and Sperry *et al.* (2017). Eller *et al.* (2020) use an analytical approximation of this stomatal algorithm in the JULES land-surface model and test the model at 70 eddy flux sites around the world. Sabot *et al.* (2020) implement the full stomatal optimization in a simplified version of the CABLE land-surface model and test different model versions and parameter assumptions at 10 flux towers during drought. Both articles show major improvements to simulation of ecosystem fluxes of water and carbon, which are very important findings, although with some variation and nuances. Both articles also include a very thorough and differing set of validation analyses against eddy flux towers and hydraulic trait datasets.

Why are these findings important? Adding complexity in biosphere models needs to be justified because it can increase computational demands and the number of parameters required to run the model, potentially decreasing model performance and increasing uncertainty. Here, however, this increase in complexity from hydraulic transport and hydraulic-based stomatal optimizations is useful, justified, and powerful because it (1) improves

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This article is a Commentary on Eller *et al.*, 226: 1622–1637 and Sabot *et al.*, 226: 1638–1655.



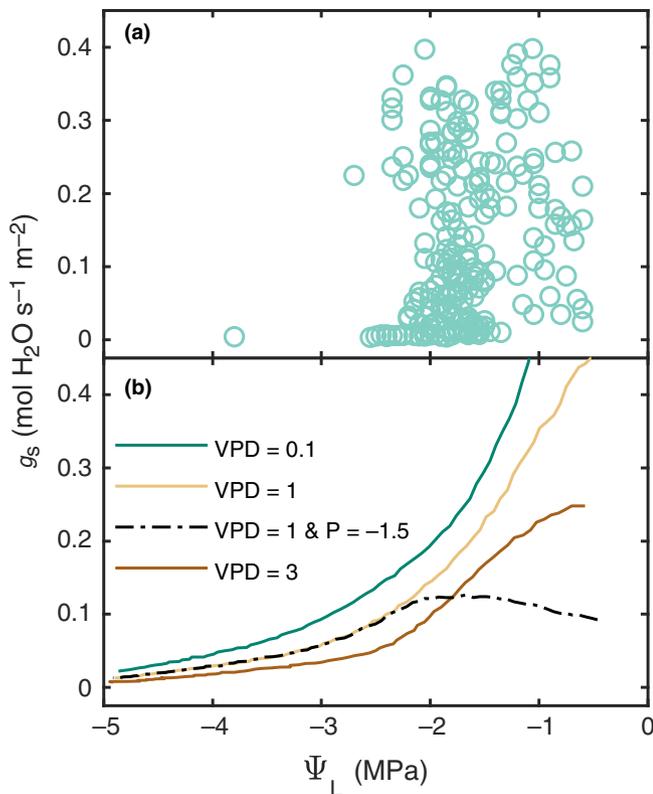
**Fig. 1** Conceptual framework illustrating previous empirical and new optimization-based formulations of stomatal conductance and water transport. (Left) Empirical approaches generally use equations similar to the Ball–Berry–Leuning model for calculating the stomatal conductance for carbon dioxide ( $\text{CO}_2$ ) diffusion ( $g_s$ ), where  $g_0$  is the minimum,  $g_s$  at the light compensation point,  $A$  is the net leaf  $\text{CO}_2$  assimilation rate,  $\text{CO}_2$  is the concentration at the leaf surface,  $\Gamma$  is the  $\text{CO}_2$  compensation point,  $D$  the vapor pressure deficit (VPD), and  $a_1$  and  $d_0$  are empirical coefficients. This equation does not take into account soil moisture content ( $\theta_{\text{soil}}$ ), thus, to link leaf responses to soil moisture  $\beta$  a function that ranges from 1 (fully open) to 0 (fully closed). This function has several shapes depending on the model used (e.g.  $\beta_1$  for JULES,  $\beta_2$  for SiB3, and  $\beta_3$  for IBIS; Powell *et al.*, 2013). (Right) Hydraulic approaches, such as Sperry *et al.* (2017), calculate supply–demand curves from soil-to-atmosphere based on the hydraulic conductivity of the elements of the pathway ( $K_{\text{rhizos}}$ ,  $K_{\text{root}}$ ,  $K_{\text{stem}}$ ,  $K_{\text{leaf}}$ , which are functions of the water potential of the element), stomatal conductance to water vapor ( $g_w = 1.6 g_s$ ), and environmental conditions (including soil and atmospheric water potentials,  $\Psi_{\text{soil}}$  and  $\Psi_{\text{air}}$ , respectively). This enables calculating the gain function as net assimilation ( $A$ ) divided by maximum net assimilation ( $A_{\text{net}}$ ) and the risk function as one minus hydraulic conductivity ( $K$ ; i.e. the vulnerability curve) divided by maximum hydraulic conductivity ( $K_{\text{max}}$ ) for that set of environmental conditions. Optimization theory is then used to determine that the plant will select a  $g_s$  that results in a canopy pressure ( $P_{\text{canopy}}$ ) that maximizes the difference between the instantaneous gain and risk.

mechanistic realism, (2) leverages large and existing datasets of hydraulic traits, and (3) decreases model parameters rather than increasing them (Fig. 1). In the models developed here, a set of *c.* 4–6 mechanistic parameters from the empirical stomatal models can be replaced by *c.* 2–3 parameters that can mostly be directly estimated from field measurements, such as the hydraulic vulnerability curve (Fig. 1). Another drawback of incorporating plant hydraulics can be increased computation time, but this is not as important due to rapid development of computation capacity and approaches such as followed by Eller *et al.* (2020) that leverages an analytical approximation. In addition, the failure of plant hydraulic transport has been broadly observed as crucial to predicting mortality risk during drought and ecosystem resilience (Adams *et al.*, 2017; Anderegg *et al.*, 2018a; Venturas *et al.*, 2018), suggesting that improved hydraulic physiology might improve multiple important aspects of biosphere models.

Based on these articles and other recent work, we posit that there are several promising future research directions and potential pitfalls moving forward. While many models are adding plant hydraulic transport, it is becoming increasingly apparent that how one links hydraulic transport with stomatal conductance might matter. One previous approach has been to link the two by making

stomatal conductance an empirical function of leaf water potential ( $g_s(\Psi_L)$ ), which is in essence a  $\beta$ -type function but using leaf water potential calculated via hydraulics rather than soil moisture or soil water potential. We suggest that this approach is not advisable for two major reasons. First, unlike the hydraulic vulnerability curve, the  $g_s(\Psi_L)$  function is not a unique curve but instead varies in different soil water potential or VPD conditions (Fig. 2). Thus, the function itself shifts depending on short-term environmental conditions, making it not a terribly useful ‘functional trait’. Second and related, this function is often incredibly noisy in real-world data and thus is a poor target for incorporating into models (Fig. 2). One major advantage of the Sperry *et al.* (2017), Eller *et al.* (2020) and Sabot *et al.* (2020) approaches is that one can entirely dispense with empirical functions of stomatal response to soil moisture, VPD, and leaf water potential, and the stomatal response is instead an emergent property based on plant traits like the vulnerability curve, photosynthetic capacity, and allocation patterns.

In terms of key future research frontiers, the ability of plants to recover from drought and hydraulic damage, via embolism refilling or other mechanisms, is an urgent need in both plant ecophysiology and modeling of plant hydraulics. Future efforts should also account for different time periods over which hydraulic damage can



**Fig. 2** (a) There is no unique stomatal conductance ( $g_s$ ) response for a given leaf water potential ( $\Psi_L$ ) as shown by data from *Populus tremuloides* (aspen) from Venturas *et al.* (2018). (b) Theoretical  $g_s$  responses predicted using the Venturas *et al.* (2018) model keeping aspen traits and environmental variables constant ( $T_{\text{air}} = 25^\circ\text{C}$ , solar radiation =  $700 \text{ W m}^{-2}$ , and wind speed =  $1 \text{ m s}^{-1}$ ) and varying soil water potential ( $\Psi_{\text{soil}}$ ) from  $-0.1$  to  $-4.0$  MPa for atmospheric vapor pressure deficits (VPDs) of 0.1, 1 and 3 kPa (solid lines). The  $g_s$  is reduced for a VPD = 1 kPa if there is no xylem refilling and the plant experienced a previous drought that reached  $\Psi_{\text{soil}} = -1.5$  MPa (black dash-dot line).

or cannot be repaired, which should help lead to more realistic modeled drought responses. In addition, we need additional research to understand and predict a key remaining model parameter – the maximum plant hydraulic conductance (termed  $k_{\text{max}}$  in Sabot *et al.*, 2020;  $r_{\text{pmin}}$  in Eller *et al.*, 2020) – across the landscape. Sabot *et al.* (2020) conduct an exploratory test and find some promising patterns of  $k_{\text{max}}$  as a function of precipitation. Also explored briefly in Sabot *et al.* (2020), the potential for acclimation and plasticity in hydraulics traits and allocation is a key research frontier. Such acclimation can likely affect many aspects of plant traits, allocation patterns, and responses to climate change (Sperry *et al.*, 2019). Considering plant hydraulics from a whole-plant perspective that includes the resistance across different tissues, trait coordination, and potential for hydraulic segmentation will be particularly important. Finally, linking hydraulics to demographic outcomes particularly drought-driven mortality at large scales remains an exciting and key research frontier.

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