

Soil-plant hydraulics explain stomatal efficiency-safety tradeoff

Gaochao Cai¹ | Andrea Carminati²  | Sean M. Gleason³  | Mathieu Javaux⁴ | Mutez Ali Ahmed^{5,6}

¹School of Agriculture, Shenzhen Campus of Sun Yat-sen University, Shenzhen, China

²Physics of Soils and Terrestrial Ecosystems, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zürich, Zurich, Switzerland

³United States Department of Agriculture, Water Management and Systems Research Unit, Agricultural Research Service, Fort Collins, Colorado, USA

⁴Earth and Life Institute-Environmental Science, Université catholique de Louvain, Louvain-la-Neuve, Belgium

⁵Chair of Soil Physics, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany

⁶Department of Land, Air and Water Resources, College of Agricultural and Environmental Sciences, University of California Davis, Davis, California, USA

Correspondence

Mutez Ali Ahmed, Chair of Soil Physics, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstraße 30, Bayreuth 95447, Germany.
Email: maaahmed@ucdavis.edu

Funding information

Deutsche Forschungsgemeinschaft

Abstract

The efficiency-safety tradeoff has been thoroughly investigated in plants, especially concerning their capacity to transport water and avoid embolism. Stomatal regulation is a vital plant behaviour to respond to soil and atmospheric water limitation. Recently, a stomatal efficiency-safety tradeoff was reported where plants with higher maximum stomatal conductance (g_{\max}) exhibited greater sensitivity to stomatal closure during soil drying, that is, less negative leaf water potential at 50% g_{\max} (ψ_{gs50}). However, the underlying mechanism of this g_{\max} - ψ_{gs50} tradeoff remains unknown. Here, we utilized a soil-plant hydraulic model, in which stomatal closure is triggered by nonlinearity in soil-plant hydraulics, to investigate such tradeoff. Our simulations show that increasing g_{\max} is aligned with less negative ψ_{gs50} . Plants with higher g_{\max} (also higher transpiration) require larger quantities of water to be moved across the rhizosphere, which results in a precipitous decrease in water potential at the soil-root interface, and therefore in the leaves. We demonstrated that the g_{\max} - ψ_{gs50} tradeoff can be predicted based on soil-plant hydraulics, and is impacted by plant hydraulic properties, such as plant hydraulic conductance, active root length and embolism resistance. We conclude that plants may therefore adjust their growth and/or their hydraulic properties to adapt to contrasting habitats and climate conditions.

KEYWORDS

leaf water potential, plant hydraulic conductance, stomatal conductance, stomatal regulation, transpiration

1 | INTRODUCTION

A paradigm in plant-water relations assumes there is a tradeoff between the maximum capacity to transport water (and achieve exchange gas) and the vulnerability of this transport system to low water potential, that is, the loss of hydraulic conductance per unit decrease in xylem

water potential. This is the so-called hydraulic efficiency-safety tradeoff, with efficiency referring to the maximum hydraulic conductance/conductivity of whole-leaves, whole-plants or xylem segments, and safety referring to the water potential at 50% loss in xylem hydraulic conductivity (P_{50} or ψ_{x50}) (Brodrick & Holbrook, 2003; Fan et al., 2011; Gleason et al., 2016; Johnson et al., 2022; Ocheltree et al., 2016;

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Plant, Cell & Environment* published by John Wiley & Sons Ltd.

Scoffoni & Sack, 2017; Yao et al., 2021). This tradeoff reflects plant responses to water stress (Choat et al., 2012) and water use strategies, and it depends on the combination of different traits (e.g., vessel density and size, stomatal density and size) (De Guzman et al., 2017; Henry et al., 2019; Schumann et al., 2019). Numerous studies have investigated the tradeoff in woody species spanning contrasting habitats and climate conditions (e.g., Gleason et al., 2016; Grossiord et al., 2020; Liu et al., 2021; Nardini & Luglio, 2014; Yan et al., 2020). However, the underlying mechanisms of such tradeoff remain largely unknown (Blackman et al., 2010; Gleason et al., 2016; Liu et al., 2021; Scoffoni et al., 2012).

Hydraulic efficiency has been shown to closely correlate with maximum stomatal conductance (Brodrribb et al., 2007; Hubbard et al., 2001; Meinzer & Grantz, 1990; Sack et al., 2003). Analysis of stomatal sensitivity and plant hydraulic vulnerability to drought across 310 woody species indicated that vulnerability to embolism was most relevant during severe drought, whereas stomatal regulation was vital during moderate drought (Bartlett et al., 2016). Additionally, Anderegg et al. (2017) and Ocheltree et al. (2016) showed that leaf water potential at 50% loss in stomatal conductance (ψ_{gs50}) was less negative than ψ_{x50} , indicating that a stomatal regulation occurred before xylem embolism.

Henry et al. (2019) investigated the stomatal efficiency-safety tradeoff through the relationship between maximum stomatal conductance (g_{max}) and ψ_{gs50} , and hypothesized that plants with smaller and denser stomata should be more conservative in their stomatal closure. They found that plants with higher g_{max} had less negative leaf water potentials than plants with lower g_{max} when g_{max} decreased by 50% as the soil dried (Figure 1a,b). The authors revealed a strong g_{max} - ψ_{gs50} tradeoff across 15 woody species (including trees and shrubs, Figure 1c). Here, we demonstrate that the tradeoff between stomatal efficiency and safety (g_{max} and ψ_{gs50}) can be predicted from well-understood aspects of soil-plant hydraulic functioning (Carminati & Javaux, 2020; Sperry &

Love, 2015). We also explore how plant hydraulic traits may affect the g_{max} - ψ_{gs50} tradeoff. We note that the proximal physiological mechanisms underpinning stomatal regulation are beyond the scope of this study, and we therefore focus here on empirical and theoretical support for coordination between stomatal conductance and soil-plant hydraulics.

2 | MODEL DESCRIPTION

2.1 | Soil-plant hydraulic model

The soil-plant hydraulic model used in this study was developed by Carminati and Javaux (2020) and has been introduced in several recent studies (Abdalla et al., 2021, 2022; Cai et al., 2020, 2021; Cai, Ahmed, et al., 2022; Hayat et al., 2020). Here, we briefly present the principle and main functions of the model. In the model, water flow from soil to plant is driven by water potential differences between bulk soil, the soil-root interface (ψ_{soil_root}), the root xylem (ψ_{root_xylem}) and the leaf (ψ_{leaf}). To simplify conversions between hydrostatic and matric water potential components, we express soil water potential (ψ_{soil}) as the height of water, that is, 1 MPa = 10^4 hPa $\approx 10^4$ cm. This is done because the water potential (total energy) of unsaturated soil is dominated by matric potential, with gravitational, osmotic and hydrostatic components being negligible in most cases. Water transport is regulated in the model by soil hydraulic conductivity (k_{soil} , $cm\ s^{-1}$) and plant hydraulic conductance (K_{plant} , including root and aboveground xylem conductance, K_{root} and K_{xylem}). Water flow from the soil towards the root is assumed to be under steady-state behaviour and the radial flux (q , $cm\ s^{-1}$) is represented by:

$$q = -k_{soil}(\psi_{soil}) \frac{\partial \psi}{\partial r}, \quad (1)$$

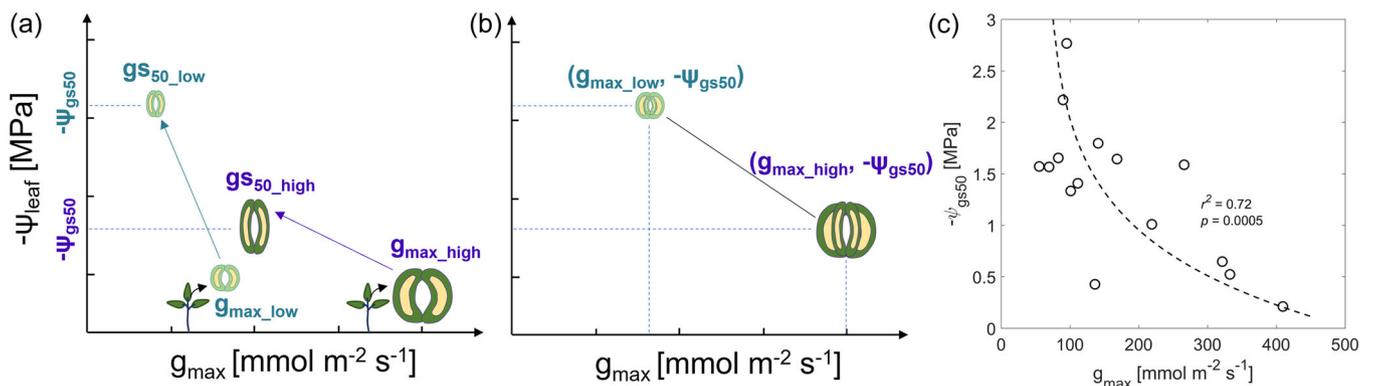


FIGURE 1 Relationship between maximum stomatal conductance (g_{max}) and the leaf water potential (ψ_{leaf}) resulting in a 50% reduction in stomatal conductance (g_{s50}). (a) Plants with higher g_{max} (g_{max_high}) reduce stomatal conductance (g_{s50}) earlier and at less negative leaf water potential (ψ_{gs50}) as soil dries. Similarly, plants with lower g_{max} (g_{max_low}) exhibit more negative leaf water potential at 50% of maximal stomatal conductance (ψ_{gs50}). (b) The hypothesized tradeoff between g_{max} and ψ_{gs50} . (c) Leaf water potential resulting in a 50% decline in stomatal conductance (ψ_{gs50}) across 15 California tree and shrub species as reported in Henry et al. (2019). Data were fitted with an exponential function as used by Henry et al. (2019) ($g_{max} = c + ae^{-b\psi_{leaf}}$). (a)–(c) are fitted parameters.

where $\frac{\partial\psi}{\partial r}$ is the gradient in soil water potential, and r is the radial distance (cm). Soil hydraulic conductivity increases with soil matric potential and can be described by the Brooks and Corey model (1964):

$$k_{\text{soil}}(\psi) = k_{\text{sat}} \left(\frac{\psi_{\text{soil}}}{\psi_0} \right)^\tau, \quad (2)$$

where k_{sat} is the soil saturated hydraulic conductivity (cm s^{-1}), ψ_0 is the air entry point (hPa) and τ is a fitted parameter.

In the rhizosphere, the boundary conditions are no water flux at the outer radius of the rhizosphere (r_b , cm) and a uniform water flux (q , $\text{cm}^3 \text{cm}^{-2} \text{s}^{-1}$) at the root surface (r_0 , cm; root radius) along the active root system. q depends on transpiration rate (E , $\text{cm}^3 \text{s}^{-1}$) and root surface:

$$q(r_0) = E / (2\pi r_0 L_{\text{act}}), \quad (3)$$

where L_{act} is defined as the fraction of root length (cm) active in water uptake. r_b is calculated from soil volume (V , cm^3) and L_{act} : $r_b = (V/\pi L_{\text{act}})^{0.5}$.

Water flow in the soil, root and xylem can be calculated individually by Ohm's law. For instance, the water flow in the soil is defined as a function of overall soil hydraulic conductance (K_{soil} , $\text{cm}^3 \text{hPa}^{-1} \text{s}^{-1}$) and water potential gradient between soil and soil-root interface:

$$E = K_{\text{soil}} (\psi_{\text{soil}} - \psi_{\text{soil_root}}), \quad (4)$$

where $\psi_{\text{soil_root}}$ is the water potential at the soil-root interface (hPa). The water flow in the root system is described by:

$$E = K_{\text{root}} (\psi_{\text{soil_root}} - \psi_{\text{xylem_root}}), \quad (5)$$

where K_{root} is the root hydraulic conductance ($\text{cm}^3 \text{hPa}^{-1} \text{s}^{-1}$), $\psi_{\text{xylem_root}}$ is the water potential at the root collar (hPa) (see details of $\psi_{\text{soil_root}}$ and $\psi_{\text{soil_root}}$ in Carminati & Javaux, 2020; Cai et al., 2021). The water flow in the aboveground xylem is defined as:

$$E = K_{\text{xylem}} (\psi_{\text{xylem_root}} - \psi_{\text{leaf}}), \quad (6)$$

where K_{xylem} is the aboveground xylem conductance ($\text{cm}^3 \text{hPa}^{-1} \text{s}^{-1}$), and $\psi_{\text{xylem_root}} - \psi_{\text{leaf}}$ is the water potential difference (driving force) between root and leaf (hPa). K_{xylem} is derived from K_{root} and declines as leaf water potential falls below the xylem embolism threshold:

$$K_{\text{xylem}}(\psi) = K_{\text{root}} \left(\frac{\psi_{\text{leaf}}}{\psi_{\text{xylem}_0}} \right)^{-\tau_x}, \quad (7)$$

where ψ_{xylem_0} is the water potential (hPa) at which emboli arise in the xylem, resulting in a decrease in K_{xylem} . τ_x is a fitted parameter. The water flow in the plant is defined as:

$$E = K_{\text{plant}} (\psi_{\text{soil_root}} - \psi_{\text{leaf}}). \quad (8)$$

Similarly, the water flow in the soil-plant system is represented by a function of soil-plant hydraulic conductance and water potential difference between soil and leaf:

$$E = K_{\text{soil_plant}} (\psi_{\text{soil}} - \psi_{\text{leaf}}). \quad (9)$$

In wet conditions, the water potential difference between the bulk soil and the root surface is negligible, thus

$$\begin{aligned} \psi_{\text{soil}} &\approx \psi_{\text{soil_root}} \text{ and } E \approx K_{\text{plant}} (\psi_{\text{soil}} - \psi_{\text{leaf}}) \\ &= K_{\text{soil_plant}} (\psi_{\text{soil}} - \psi_{\text{leaf}}). \end{aligned} \quad (10)$$

Equation (9) implies that when transpiration is null, leaf water potential equals soil water potential. In wet soils and at low transpiration rates, the leaf water potential drops linearly with increasing transpiration rate (Figure 2a). In wet soils, the linearity is maintained at high transpiration rates unless plant hydraulic conductance drops. Sperry and Love (2015) used a supply-demand function concept to propose that stomata would ensure that the ratio between transpiration rate and the difference between leaf and soil water potential (Equation 10) remains constant. As the soil dries out, that is, soil water potential decreases, the transpiration rate-leaf water potential ($E(\psi_{\text{leaf}})$) relationship starts to deviate from the linearity at moderate transpiration rates due to the drop in soil hydraulic conductivity (Carminati & Javaux, 2020). This deviation marks the transition of the $E(\psi_{\text{leaf}})$ relationship from the linear (green) to nonlinear (yellow) zones (Figure 2a).

Carminati and Javaux (2020) defined the onset of nonlinearity as the stress onset limit (SOL). The SOL curve is composed of points at which the slope of the $E(\psi_{\text{leaf}})$ relationship at a constant soil water potential reaches 60%–80% of its maximum, $\text{SOL}(\psi_{\text{soil}}) = \frac{\partial E}{\partial \psi_{\text{leaf}}} / \psi_{\text{soil}}$. The rational and the proposed physiological mechanism underpinning the nonlinear portion of the $E(\psi_{\text{leaf}})$ relationship is discussed at length in Wankmüller and Carminati (2022). Similar to Sperry and Love (2015), we propose that stomata respond to the change in transpiration rate relative to the change in leaf water potential (i.e., $\frac{\partial E}{\partial \psi_{\text{leaf}}}$) to maintain the plant in the linear zone of the $E(\psi_{\text{leaf}})$ relationship. By staying in the linear zone of this relationship, plants avoid precipitous decline in leaf water potential as the transpiration rate increases, thus avoiding hydraulic failure, that is, embolism formation. The SOL is, therefore, the hypothetical maximum transpiration rate that can be achieved without incurring high embolism risk. Plants with different maximum transpiration rates (or g_{max}) but identical hydraulic conductance and root length, exhibited the same SOL curve, but the peak of the curve was determined by the maximum transpiration rate (Figure 2b).

2.2 | Stomatal model

We used the soil-plant hydraulic model to test whether it could explain the $g_{\text{max}}-\psi_{g50}$ tradeoff shown in Figure 2. We ran several scenarios at steady-state with the parameters provided in Table 1.

Stomatal conductance (g_s) was calculated from transpiration rate (E), leaf area (LA), vapour pressure deficit (VPD) and atmospheric pressure (P_{atm}) according to Jarvis and McNaughton (1986), that is, $g_s = (E/LA)/(VPD/P_{atm})$. g_s corresponds to g_{max} when E is maximal and to g_{s50} when E decreases by 50%. We assumed that the plants have the same leaf area and similar response to VPD (Oren et al., 1999) thus the simulations were run at the same P_{atm} and VPD (Table 1).

3 | SOIL-PLANT HYDRAULICS EXPLAIN THE STOMATAL EFFICIENCY-SAFETY TRADEOFF

Our simulations show that increasing maximum stomatal conductance (g_{max}) resulted in a 50% reduction in stomatal conductance at less negative water potential. This demonstrates that the g_{max} - ψ_{gs50} tradeoff

FIGURE 2 Illustration of the stomatal efficiency-safety tradeoff using the soil-plant hydraulic model. (a) Transpiration rate (E) as a function of leaf water potential (ψ_{leaf}) during soil drying. The red curve is the stress onset limit line (SOL) that separates the $E(\psi_{leaf})$ relationship into linear (green) and nonlinear (yellow) zones. (b) Relationship between transpiration rate and leaf water potential for plants with a higher (purple) and lower (green) maximum stomatal conductance during soil drying. (c) Combination of (a) and (b) with stomatal conductance at 50% of their maximum (g_{s50}). (d) Relationship between g_{max} and leaf water potential when g_{max} drops by 50% (ψ_{gs50}). The blue and green points are from (c). (e) Relationship between leaf water potential at midday (ψ_{leaf_MD}) and predawn (ψ_{leaf_PD}) of plants with high and low g_{max} . (f) Relationship between the soil water potential and water potential at the soil-root interface with increasing E at g_{max} and g_{s50} considering plants with high and low g_{max} . The data at g_{max} and g_{s50} are highlighted using open and closed symbols, respectively. The same parameters were used in the simulation in (a-f), and the parameters are described in Table 1. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

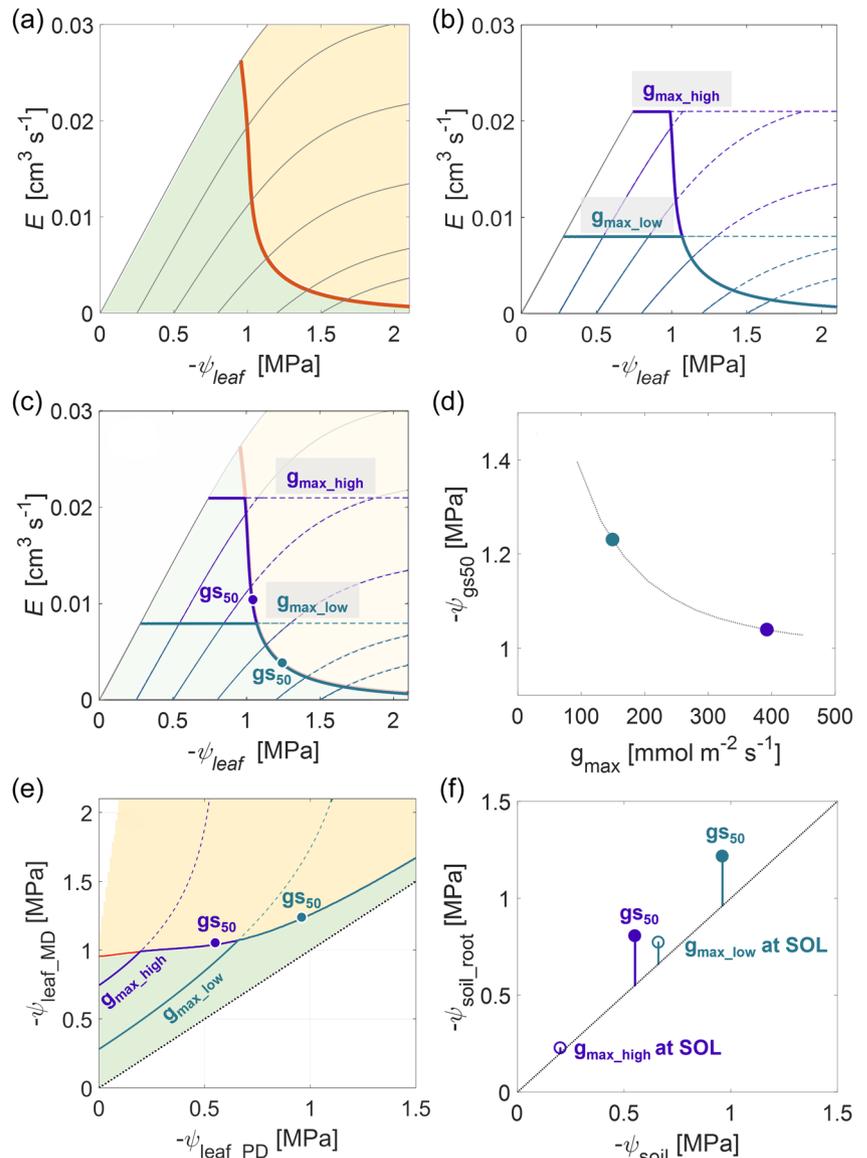


TABLE 1 Values of the parameters in the soil-plant hydraulic model (Carminati & Javaux, 2020) in Figure 2

	Equation	Parameter ^a
Soil	$k_{soil}(\psi) = k_{sat} (\psi_{soil}/\psi_o)^{-\tau}$	k_{sat} : $2.1 \times 10^{-4} \text{ cm s}^{-1}$; $\psi_o = -8.3 \text{ cm}$; $\tau = 2$
Soil root domain		$r_o = 0.05 \text{ cm}$; $r_b = 1 \text{ cm}$; $L_{act} = 10\,000 \text{ cm}$
Plant xylem and leaf	$K_x(\psi) = K_{plant} (\psi/\psi_{ox})^{-\tau_x}$	$K_{plant} = 1/(3.5 \times 10^5) \text{ cm}^3 \text{ s}^{-1} \text{ hPa}^{-1}$; $\psi_{ox} = \psi_{x50} = 1.8 \text{ Mpa}$; $\tau_x = 5$ $E_{max_high} = 0.021 \text{ cm}^3 \text{ s}^{-1}$; $E_{max_low} = 0.008 \text{ cm}^3 \text{ s}^{-1}$

^a $g_{max} = (E_{max}/LA)/(VPD/P_{atm})$. Leaf area (LA) is 2000 cm^2 , vapour pressure deficit (VPD) is 1.5 kPa and P_{atm} is the atmospheric pressure, 101 kPa . Soil parameters are from Abdalla et al. (2021). K_{plant} is based on Anderegg et al. (2018) and Cai, Ahmed, et al. (2022).

can be simulated using the soil-plant hydraulic model by changing only the value of g_{\max} (Figure 2c,d). This should make sense because plants with higher g_{\max} (also higher transpiration rate) require larger quantities of water to be moved across the root zone, which results in a precipitous decrease in the water potential at the soil-root interface, and therefore also in the leaves. As the soil dries, water potential (and soil hydraulic conductivity) at the soil-root interface decreases markedly (Figure 2f) (Cai, Ahmed, et al., 2022; Carminati & Vetterlein, 2013) and becomes the main constraint on water flux. Importantly, higher water flux across the soil-root interface resulted in plants reaching the SOL sooner than plants with less water flux across the soil-root interface (Figure 2b,c). We suggest that this nonlinear portion of the transpiration rate-leaf water potential function (i.e., points on the SOL curve) represents a critical moment for plants because leaf water potential can decrease faster than stomata guard cells can respond hydroactively (Buckley, 2019). We should therefore expect a rapid stomatal response when the SOL is approached to avoid a sudden drop in water potential at the root-soil interface (Carminati & Ahmed, Zarebanadkouki, et al., 2020) and the possible permanent embolization of xylem tissue. Given that soil conductivity declines precipitously before xylem embolism, and that stomata are well-positioned to slow the loss of water from the canopy, it is logical that species exhibiting higher g_{\max} might also require more conservative stomata (less negative ψ_{gs50}) to avoid operating too far beyond the SOL. Indeed, plants with higher g_{\max} exhibit earlier stomatal closure during soil drying, that is, higher stomatal efficiency but lower stomatal safety (Figures 1 and 2d).

In the simulation described above, and as observed in species across the day, values of transpiration rate, soil matric potential, and leaf water potential at the SOL point are well aligned with the leaf water potential at midday and at predawn. The 1:1 line where predawn leaf water potential equals soil matric potential ($\psi_{leaf_PD} = \psi_{soil}$) and the SOL curve delimit a region in the hydroscape domain (green zone in Figure 2e) where stomatal regulation is not constrained by plant hydraulic status (Javaux & Carminati, 2021). In this region, plants with higher g_{\max} show more negative midday leaf water potential than plants with lower g_{\max} . As the soil dries, the loss in soil hydraulic conductivity induces stomatal closure (Abdalla et al., 2022; Cai, König, et al., 2022; Carminati & Javaux, 2020; Koehler et al., 2022) and maintains midday leaf water potential very close to the SOL curve. Plants with high g_{\max} reach the SOL curve at less negative predawn leaf water potential (i.e., in wetter soils) than species with low g_{\max} , but the corresponding midday leaf water potential of species with high g_{\max} was not as negative as species exhibiting lower g_{\max} (Figure 2e,f).

4 | IMPACT OF PLANT HYDRAULIC PARAMETERS ON THE STOMATAL EFFICIENCY-SAFETY TRADEOFF

The discussion above was based on the assumptions of constant plant hydraulic conductance and root length. However, different genotypes or species may show coordination between g_{\max} , plant hydraulic conductance and root length. Additionally, plants that differ

in water potential at 50% of xylem hydraulic conductivity (ψ_{x50}) would also shift the SOL curve (Carminati & Javaux, 2020) and thus impact the g_{\max} - ψ_{gs50} relationship. We further used the soil-plant hydraulic model to predict the impact of these parameters on the g_{\max} - ψ_{gs50} tradeoff. We investigated three scenarios: (1) changing plant hydraulic conductance with a constant root length and ψ_{x50} , (2) changing root length with a constant plant hydraulic conductance and ψ_{x50} and (3) changing ψ_{x50} with a constant root length and plant hydraulic conductance. The corresponding parameters are presented in Table 2.

In the first scenario, we increased plant hydraulic conductance by a factor of 2.25 and increased g_{\max} by a factor of either 2.1 (high g_{\max}) or 1.5 (low g_{\max}) (Figure 3a). For both high and low g_{\max} , ψ_{gs50} became more negative with increasing plant hydraulic conductance, particularly for plants with high g_{\max} (Figure 3b). Lower plant hydraulic conductance 'pushed' the relationship to the left corner (golden arrow in Figure 3b) and plants with high and low g_{\max} showed less stomatal efficiency but more safety. An increase in plant hydraulic conductance did not change the tradeoff and even made the g_{\max} - ψ_{gs50} relation more marked. Higher plant hydraulic conductance increased the sensitivity of stomatal closure to drops in soil hydraulic conductivity around the roots.

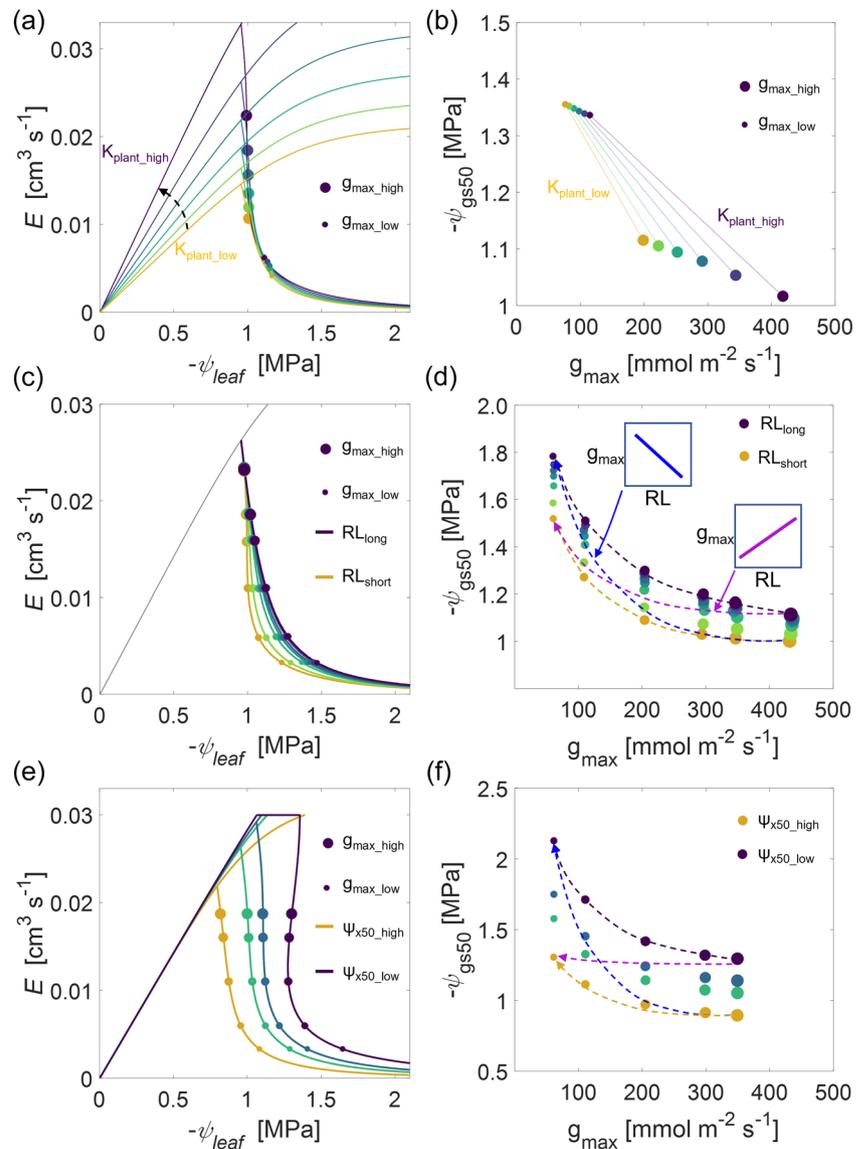
In the second scenario, we tested the impact of increasing root length by a factor of 10 (Figure 3c). We used the same g_{\max} as Figure 2c. Increasing root length resulted in a reduction in ψ_{gs50} , indicating that plants with longer root length maintained relatively high stomatal conductance during soil drying (Figure 3d). This is due to longer root length which slows down water flux in soil and reduces the gradient in water potential at the soil-root interface (Abdalla et al., 2022; Cai et al., 2021). Hence, plants are able to maintain transpiration at lower soil matric potentials and postpone stomatal closure (Abdalla et al., 2022). When root length increased by the same factor, the reduction in ψ_{gs50} was greater for plants with lower

TABLE 2 Values of the parameters in the soil-plant hydraulic model for the sensitivity analyses in Figure 3

	Parameter ^a	Value
Figure 3a,b	K_{plant}	$1/(3.5 \times 10^5 \times [0.8, 1, 1.2, 1.4, 1.6, 1.8]) \text{ cm}^3 \text{ s}^{-1} \text{ hPa}^{-1}$
	$E_{\text{max_high}}$	0.01 and 0.022 $\text{cm}^3 \text{ s}^{-1}$ at the lowest and highest K_{plant} above
	$E_{\text{max_low}}$	0.005 and 0.011 $\text{cm}^3 \text{ s}^{-1}$ at the lowest and highest K_{plant} above
Figure 3c,d	L_{act}	$10\,000 \times [0.8, 1, 1.5, 2, 2.5, 4, 8] \text{ cm}$
	E_{max}	$[0.0032, 0.0056, 0.011, 0.015, 0.018, 0.023] \text{ cm}^3 \text{ s}^{-1}$
Figure 3e,f	ψ_{x50}	$[-1.5, -1.8, -2.0, -2.5] \text{ MPa}$
	E_{max}	$[0.0032, 0.0056, 0.011, 0.015, 0.018] \text{ cm}^3 \text{ s}^{-1}$

^aValues of other parameters not mentioned here are the same as those in Table 1.

FIGURE 3 Sensitivity analysis of the g_{\max} - ψ_{gs50} relationship to the changes of plant hydraulic conductance (K_{plant}), active root length (RL) and water potential at 50% maximal xylem conductivity (ψ_{x50}). (a) Changes of g_{\max} with increasing K_{plant} by a factor of 2.25. (b) Variation in the g_{\max} - ψ_{gs50} relationship with increasing K_{plant} in (a). The line between $g_{\max_{\text{high}}}$ (large point) and $g_{\max_{\text{low}}}$ (small point) shows the trend and does not necessarily mean that the relationship is linear. (c) Changes of g_{\max} with increasing active root length (RL) by a factor of 10 (seven lines in total). The slight deviation of g_{\max} at the same level resulted from using the resolution of E at $1 \times 10^{-5} \text{ cm}^3 \text{ s}^{-1}$. (d) Variation in the g_{\max} - ψ_{gs50} relationship with increasing RL (golden to dark purple) in (c). The golden and dark purple arrows represent the g_{\max} - ψ_{gs50} relationships with short and long root lengths, respectively. The blue arrow represents that relationship when taking higher g_{\max} with a shorter root length and lower g_{\max} with a longer root length, whereas the purple represents the opposite. (e) Changes of g_{\max} with increasing ψ_{x50} . (f) Variation in the g_{\max} - ψ_{gs50} relationship with decreasing ψ_{x50} in (e). The arrows with different colours represent similar cases as those in (d). All the parameters used in the simulations are presented in Table 2. [Color figure can be viewed at wileyonlinelibrary.com]



g_{\max} than with higher g_{\max} , which resulted in a steeper negative slope (blue arrow in Figure 3d). It is worth noting that the effect of increasing root length on ψ_{gs50} (or the tradeoff) is limited when root length increases above a certain level. Note that these are the cases when all the g_{\max} values are distributed on the same SOL curve. We also examined the g_{\max} - ψ_{gs50} tradeoff when g_{\max} is either positively or negatively correlated with root length. When root length and g_{\max} are negatively correlated (brown arrow in Figure 3d), the slope of the tradeoff is slightly steeper compared to that when g_{\max} and root length are positively correlated (purple arrow in Figure 3d). This comparison also implies that the g_{\max} - ψ_{gs50} tradeoff would be maintained for the plants that may develop different root length under various conditions. Specifically, root length changes the sensitivity of stomatal closure within a certain range but does not change the overall g_{\max} - ψ_{gs50} relationship.

The two cases discussed above demonstrated that developing more conductive plant tissues (higher plant hydraulic conductance) makes plants with higher g_{\max} more sensitive to stomatal closure (less

negative ψ_{gs50}), while developing longer root length postpones stomatal closure more markedly in plants with lower g_{\max} . However, the individual changes in plant hydraulic conductance or root length do not change the overall tradeoff.

In the third scenario, we decreased ψ_{x50} from -1.5 to -2.5 MPa (Figure 3e). The simulation shows that lower ψ_{x50} shifted the SOL curve to a more negative leaf water potential. Hence, plants with the same g_{\max} had a more negative leaf water potential and also resulted in a reduction in ψ_{gs50} (Figure 3f). The reduction in ψ_{gs50} was greater for lower g_{\max} (left side) than for higher g_{\max} (right side), which resulted in a steeper negative slope (blue arrow in Figure 3f). Note that these are the cases when all the g_{\max} values are distributed on the same SOL curve. When g_{\max} values are on different SOL curves, for instance, when g_{\max} and ψ_{x50} are positively correlated (brown arrow in Figure 3f), the slope of the tradeoff is much steeper. However, when g_{\max} and ψ_{x50} are negatively correlated (purple arrow in Figure 3f), there is a weak or no tradeoff. In the simulation above, ψ_{x50} functions like a 'buffer zone' for ψ_{gs50} because it determines how negative ψ_{gs50} can be for a given g_{\max} .

Unlike plant hydraulic conductance and active root length, variation in ψ_{x50} may maintain the g_{\max} - ψ_{gs50} tradeoff but may reduce the slope of this relationship. Given that these are simulation results, they should be tested empirically among different plant species grown under various soil and climatic conditions.

5 | CONCLUSIONS

We demonstrated that soil-plant hydraulics are well aligned with the observed stomatal efficiency-safety tradeoff. Plants with high transpiration rates have a larger drop in water potential (or hydraulic conductivity) in the rhizosphere, which in return limits water flux from the soil to the roots at less negative soil matric potential compared to plants with a lower water uptake flux. Earlier stomatal closure would be a convenient strategy for plants with a high water flux to save water, at a cost of shoot (or leaf) growth and vice versa. Besides stomatal regulation, plants have additional or alternative strategies to adapt to water limitations, for instance, by altering their root hydraulic conductance and/or active root length. In addition, differences in the leaf water potential associated with a 50% drop in xylem conductance impact the relationship between stomatal conductance and stomatal closure. Although these strategies and impacts were evident in our simulations, they remain largely unexplored in real plants growing under natural conditions. Furthermore, plants may have other strategies that manifest over longer time periods, for instance, changes in leaf/root development or leaf-to-root ratio, which are not discussed in this study but are important research questions for the future. Exploring the hydraulic trait adaptations among species and across contrasting soil types will improve our understanding of below- and aboveground interactions during drought.

ACKNOWLEDGEMENTS

We thank the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) for funding the priority programme 2089, project number 403670197 'Emerging effects of root hairs on plant scale soil water relations' to M. A. A.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Andrea Carminati  <http://orcid.org/0000-0001-7415-0480>

Sean M. Gleason  <http://orcid.org/0000-0002-5607-4741>

REFERENCES

- Abdalla, M., Ahmed, M.A., Cai, G., Wankmüller, F., Schwartz, N., Litig, O. et al. (2022) Stomatal closure during water deficit is controlled by below-ground hydraulics. *Annals of Botany*, 129, 161–170.

- Abdalla, M., Carminati, A., Cai, G., Javaux, M. & Ahmed, M.A. (2021) Stomatal closure of tomato under drought is driven by an increase in soil-root hydraulic resistance. *Plant, Cell & Environment*, 44, 425–431.
- Anderegg, W.R.L., Wolf, A., Arango-Velez, A., Choat, B., Chmura, D.J., Jansen, S. et al. (2017) Plant water potential improves prediction of empirical stomatal models. *PLoS One*, 12, e0185481.
- Anderegg, W.R.L., Wolf, A., Arango-Velez, A., Choat, B., Chmura, D.J., Jansen, S. et al. (2018) Woody plants optimise stomatal behaviour relative to hydraulic risk. *Ecology Letters*, 21, 968–977.
- Bartlett, M.K., Klein, T., Jansen, S., Choat, B. & Sack, L. (2016) The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. *Proceedings of the National Academy of Sciences*, 113, 13098–13103.
- Blackman, C.J., Brodribb, T.J. & Jordan, G.J. (2010) Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *New Phytologist*, 188, 1113–1123.
- Brodribb, T.J., Feild, T.S. & Jordan, G.J. (2007) Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physiology*, 144, 1890–1898.
- Brodribb, T.J. & Holbrook, N.M. (2003) Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiology*, 132, 2166–2173.
- Brooks, R.H. & Corey, A.T. (1964) *Hydraulic properties of porous media*. Civil Engineering Department, Colorado State University, Fort Collins, CO. Hydrology Paper No. 3.
- Buckley, T.N. (2019) How do stomata respond to water status? *New Phytologist*, 224, 21–36.
- Cai, G., Ahmed, M.A., Abdalla, M. & Carminati, A. (2022) Root hydraulic phenotypes impacting water uptake in drying soils. *Plant, Cell & Environment*, 45, 650–663.
- Cai, G., Ahmed, M.A., Dippold, M.A., Zarebanadkouki, M. & Carminati, A. (2020) Linear relation between leaf xylem water potential and transpiration in pearl millet during soil drying. *Plant and Soil*, 447, 565–578.
- Cai, G., Carminati, A., Abdalla, M. & Ahmed, M.A. (2021) Soil textures rather than root hairs dominate water uptake and soil-plant hydraulics under drought. *Plant Physiology*, 187, 858–872.
- Cai, G., König, M., Carminati, A., Abdalla, M., Javaux, M., Wankmüller, F. et al. (2022) Transpiration response to soil drying and vapor pressure deficit is soil texture specific. *Plant and Soil*, 17. <https://doi.org/10.1007/s11104-022-05818-2>
- Carminati, A., Ahmed, M.A., Zarebanadkouki, M., Cai, G., Lovric, G. & Javaux, M. (2020) Stomatal closure prevents the drop in soil water potential around roots. *New Phytologist*, 226, 1541–1543.
- Carminati, A. & Javaux, M. (2020) Soil rather than xylem vulnerability controls stomatal response to drought. *Trends in Plant Science*, 25, 868–880.
- Carminati, A. & Vetterlein, D. (2013) Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resources. *Annals of Botany*, 112, 277–290.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R. et al. (2012) Global convergence in the vulnerability of forests to drought. *Nature*, 491, 752–755.
- Fan, D.-Y., Jie, S.-L., Liu, C.-C., Zhang, X.-Y., Xu, X.-W., Zhang, S.-R. et al. (2011) The trade-off between safety and efficiency in hydraulic architecture in 31 woody species in a karst area. *Tree Physiology*, 31, 865–877.
- Gleason, S.M., Westoby, M., Jansen, S., Choat, B., Hacke, U.G., Pratt, R.B. et al. (2016) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist*, 209, 123–136.
- Grossiord, C., Ulrich, D.E.M. & Vilagrosa, A. (2020) Controls of the hydraulic safety-efficiency trade-off. *Tree Physiology*, 40, 573–576.

- De Guzman, M.E., Santiago, L.S., Schnitzer, S.A. & Álvarez-Cansino, L. (2017) Trade-offs between water transport capacity and drought resistance in neotropical canopy liana and tree species. *Tree Physiology*, 37, 1404–1414.
- Hayat, F., Ahmed, M.A., Zarebanadkouki, M., Javaux, M., Cai, G. & Carminati, A. (2020) Transpiration reduction in maize (*Zea mays* L) in response to soil drying. *Frontiers in Plant Science*, 10, 1695.
- Henry, C., John, G.P., Pan, R., Bartlett, M.K., Fletcher, L.R., Scoffoni, C. et al. (2019) A stomatal safety-efficiency trade-off constrains responses to leaf dehydration. *Nature Communications*, 10, 3398.
- Hubbard, R.M., Ryan, M.G., Stiller, V. & Sperry, J.S. (2001) Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant, Cell & Environment*, 24, 113–121.
- Jarvis, P.G. & McNaughton, K.G. (1986) Stomatal control of transpiration: scaling up from leaf to region. In: Ford, E.D. & MacFadyen, A. (Eds.) *Advances in ecological research*. Academic Press.
- Javaux, M. & Carminati, A. (2021) Soil hydraulics affect the degree of isohydrity. *Plant Physiology*, 186, 1378–1381.
- Johnson, D.M., Katul, G. & Domec, J.-C. (2022) Catastrophic hydraulic failure and tipping points in plants. *Plant, Cell & Environment*, 45, 2231–2266.
- Koehler, T., Moser, D.S., Botezatu, Á., Murugesan, T., Kaliamoorthy, S., Zarebanadkouki, M. et al. (2022) Going underground: soil hydraulic properties impacting maize responsiveness to water deficit. *Plant and Soil*, 478, 43–58.
- Liu, H., Ye, Q., Gleason, S.M., He, P. & Yin, D. (2021) Weak tradeoff between xylem hydraulic efficiency and safety: climatic seasonality matters. *New Phytologist*, 229, 1440–1452.
- Meinzer, F.C. & Grantz, D.A. (1990) Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant, Cell & Environment*, 13, 383–388.
- Nardini, A. & Luglio, J. (2014) Leaf hydraulic capacity and drought vulnerability: possible trade-offs and correlations with climate across three major biomes. *Functional Ecology*, 28, 810–818.
- Ocheltree, T.W., Nippert, J.B. & Prasad, P.V.V. (2016) A safety vs efficiency trade-off identified in the hydraulic pathway of grass leaves is decoupled from photosynthesis, stomatal conductance and precipitation. *New Phytologist*, 210, 97–107.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N. et al. (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell & Environment*, 22, 1515–1526.
- Sack, L., Cowan, P.D., Jaikumar, N. & Holbrook, N.M. (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant, Cell & Environment*, 26, 1343–1356.
- Schumann, K., Leuschner, C. & Schuldt, B. (2019) Xylem hydraulic safety and efficiency in relation to leaf and wood traits in three temperate *Acer* species differing in habitat preferences. *Trees*, 33, 1475–1490.
- Scoffoni, C., McKown, A.D., Rawls, M. & Sack, L. (2012) Dynamics of leaf hydraulic conductance with water status: quantification and analysis of species differences under steady state. *Journal of Experimental Botany*, 63, 643–658.
- Scoffoni, C. & Sack, L. (2017) The causes and consequences of leaf hydraulic decline with dehydration. *Journal of Experimental Botany*, 68, 4479–4496.
- Sperry, J.S. & Love, D.M. (2015) What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist*, 207, 14–27.
- Wankmüller, F.J.P. & Carminati, A. (2022) Stomatal regulation prevents plants from critical water potentials during drought: result of a model linking soil-plant hydraulics to abscisic acid dynamics. *Ecohydrology*, 15, e2386.
- Yan, C.-L., Ni, M.-Y., Cao, K.-F. & Zhu, S.-D. (2020) Leaf hydraulic safety margin and safety-efficiency trade-off across angiosperm woody species. *Biology Letters*, 16, 20200456.
- Yao, G.-Q., Nie, Z.-F., Zeng, Y.-Y., Waseem, M., Hasan, M.M., Tian, X.-Q. et al. (2021) A clear trade-off between leaf hydraulic efficiency and safety in an aridland shrub during regrowth. *Plant, Cell & Environment*, 44, 3347–3357.

How to cite this article: Cai, G., Carminati, A., Gleason, S.M., Javaux, M. & Ahmed, M.A. (2023) Soil-plant hydraulics explain stomatal efficiency-safety tradeoff. *Plant, Cell & Environment*, 46, 3120–3127. <https://doi.org/10.1111/pce.14536>