Trends in Plant Science

CellPress REVIEWS

Opinion

Soil Rather Than Xylem Vulnerability Controls Stomatal Response to Drought

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The current trend towards linking stomata regulation to plant hydraulics emphasizes the role of xylem vulnerability. Using a soil–plant hydraulic model, we show that xylem vulnerability does not trigger stomatal closure in medium-wet to dry soils and we propose that soil hydraulic conductivity loss is the primary driver of stomatal closure. This finding has two key implications: transpiration response to drought cannot be derived from plant traits only and is related to soil–root hydraulics in a predictable way; roots and their interface with the soil, the rhizosphere, are key hydraulic regions that plants can alter to efficiently adapt to water limitations. We conclude that connecting below- and aboveground hydraulics is necessary to fully comprehend plant responses to drought.

Highlights

There is an increasing need for mechanistic and predictive models of transpiration and stomatal response to drought and soil water availability. It has been hypothesized that stomatal regulation is predictable based on plant and soil hydraulics.

The current trend towards a greater consideration of plant hydraulics in earth system science emphasizes xylem vulnerability, neglecting the explicit role of soil and root hydraulics.

The importance of root and soil hydraulic conductivity on plant water status is well accepted, but difficult to measure.

There is increasing evidence that plants adapt the conductivity of their roots as well as that of the soil in their vicinity, the rhizosphere, to match the soil conditions and atmospheric water demand, contributing to the regulation of plant water status and transpiration.

Soil–Root Hydraulics and Stomatal Regulation

Stomatal regulation controls most plant carbon acquisition and, thus, terrestrial productivity at the global scale. It also regulates water fluxes from the soil to the atmosphere through plants. While plant transpiration is a key driver of the hydrological cycle, its estimates suffer from large uncertainty, spanning 35–80% of terrestrial evapotranspiration [1–3]. This uncertainty arises from the difficulty of estimating stomatal conductance, in particular under drought stress.

Stomata are present on all land plants and are key features for vascular plant water content regulation on Earth. Their primary function is thought to prevent cavitation in the vascular system [4]. This function requires stomata to respond to the xylem water potential. Two main mechanisms have been demonstrated: a passive mechanism induced by the hydraulic connection between epidermal and guard cells; and an active mechanism through the production of hormones, such as abscisic acid (ABA) [5]. Sensitivity to hydraulic and hormonal signals differs between plant species and results in varying degrees of iso- and anisohydricity; these definitions indicate the capacity of plants to regulate stomatal conductance to maintain a constant (isohydricity) or less constant (anisohydricity) leaf water potential [6]. Existing models of stomatal response to drought are based on either optimization principles [7–9] or the mechanistic description of guard cell dynamics [10,11]. Despite great progress in these models [12,13], the mechanism of how soil drying impacts stomatal conductance remains unclear and existing models are empirical [14] and overestimate stomata conductance during drought [15].

An intriguing hypothesis is that stomata regulation prevents plants from exceeding the water supply function determined by soil–plant hydraulics [8]. To accomplish this function, stomata should respond to a change in transpiration in relation to a change in leaf water potential (i.e., $\frac{\partial E}{\partial \psi_{leaf}}$) (see Table 1 for definition of terms used in this article). Sperry and Love [16] argued that, in view of the uncertainty around hydraulic conductivities of dry soils and in the area of water adsorbing roots, it is pragmatic to assume that 'root investment is just sufficient to

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Table 1. Summary of Terms Used in This Article

Term	Definition	Unit of measurement
E	Transpiration flow	$m^3\ s^{-1}$
g	Gravitational acceleration	$m\ s^{-2}$
H	Water potential per weight (water head)	m
h	Soil matric potential	m
K	Hydraulic conductance	$m^3\ s^{-1}\ MPa^{-1}$
k	Hydraulic conductivity	$m\ s^{-1}$
K_{root}	Root hydraulic conductance	$cm^3\ s^{-1}\ hPa^{-1}$
k_{sat}	Saturated soil hydraulic conductivity	$m\ s^{-1}$
k_{soil}	Soil hydraulic conductivity	$m\ s^{-1}$
K_x	Aboveground xylem conductance	$m^3\ s^{-1}\ MPa^{-1}$
L	Root length	m
q	Flux or flux density	$m^3m^{-2}\ s^{-1}$
ρ	Water density	$kg\ m^{-3}$
r_0	Root radius	m
r_b	Rhizosphere radius	m
Se	Saturation index	–
S_{leaf}	Partial derivative of transpiration with respect to ψ_{leaf} for a given soil water potential	$m^3\ s^{-1}\ MPa^{-1}$
θ	Volumetric water content	m^3m^{-3}
ψ	Water potential per volume (water pressure)	MPa
ψ_{gs50}	Water potential at which stomata close by 50%	MPa
ψ_{H50}	Water potential at which soil–plant system loses 50% of its conductivity	MPa
ψ_{leaf}	Leaf water potential	MPa
$\psi_{leaf,predawn}$	Predawn leaf water potential	MPa
ψ_{s50}	Water potential at which soil loses 50% of its conductivity	MPa
ψ_{soil}	Bulk soil water potential	Mpa
ψ_{x50}	Water potential at which xylem loses 50% of its maximal conductivity	MPa

approach the xylem limit'. Behind this assumption, there is the hypothesis that plants adjust their root architecture to adapt to varying soil properties (e.g., soil texture). It follows, for these authors, that xylem cavitation, rather than soil drying, limits the water fluxes and triggers stomata closure. However, stomata were found to close much before the xylem cavitates; that is, the leaf water potential at which stomata close by 50% (ψ_{gs50}) is less negative than the water potential at which the xylem loses 50% of its conductivity (ψ_{x50}) [15]. It follows that ψ_{x50} is not informative for predicting stomatal closure.

Here, we claim that the loss of soil hydraulic conductivity, more than xylem vulnerability to embolism, is the primary constraint on transpiration during drought. It follows that ψ_{gs50} is not only a function of leaf traits, such as the maximum stomata conductance [17], or xylem vulnerability, such as ψ_{x50}, but also depends on soil–root hydraulics. In particular, we propose that stomata close when the water potential around the roots drops more rapidly than the increase in transpiration. We support this opinion with data from the literature covering different species and a hydraulic model of water flow across soil and plants (Figure 1, Key Figure).

Key Figure

Soil Drying Constraints on Stomatal Conductance and Transpiration

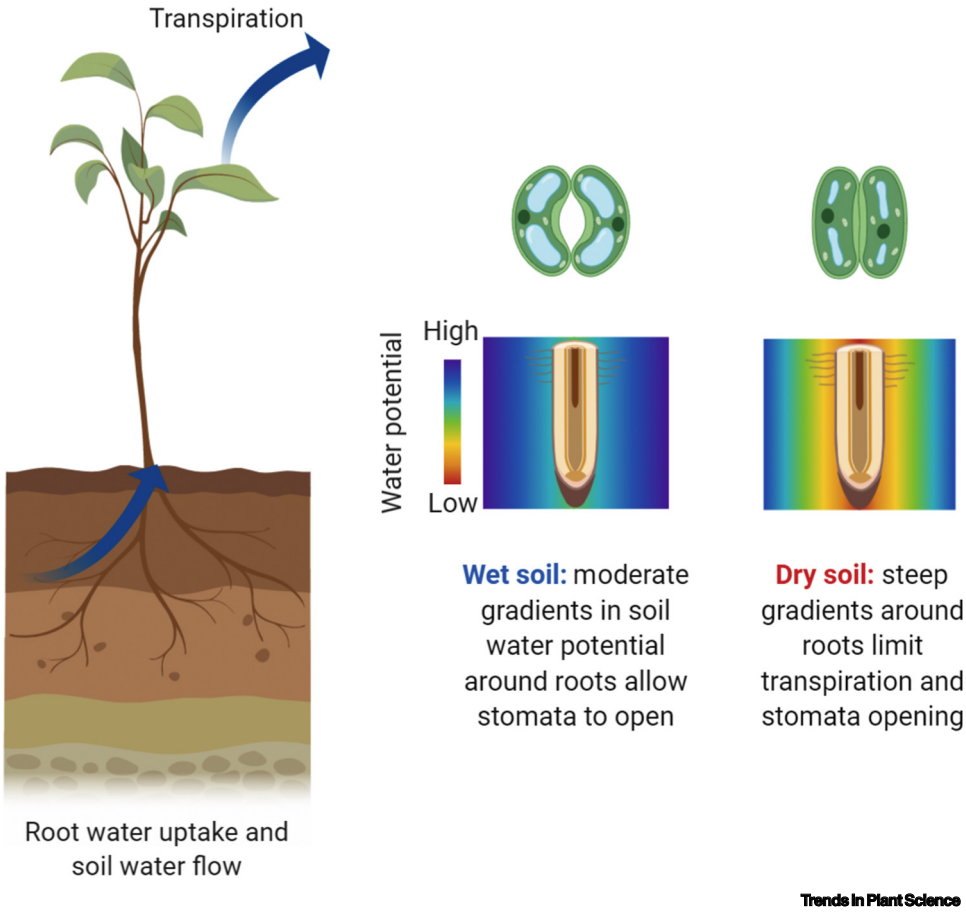

Figure 1. In wet soils, the soil hydraulic conductivity is higher than the flow velocity of soil water at the root–soil interface, the gradients in water potential around the roots are small, and the relation between transpiration and leaf water potential is linear. Under these conditions, stomata can fully open. In dry soils, the soil hydraulic conductivity drops by several orders of magnitude and the gradients in water potential around the roots become steep (Figure 2B in the main text). At this point, the leaf water potential starts to drop rapidly, unless stomata promptly close. We propose that stomata close at the onset of soil hydraulic nonlinearity. Created with BioRender (www.biorender.com).

Soil–Plant Water Fluxes

Water flows through the soil–plant–atmosphere continuum driven by a gradient in water potential, which depends on the water flow rate and the hydraulic conductivity of the different pathways. The transpiration rate is set by atmospheric conditions and, on a short timescale, is regulated by stomatal opening and closing. The hydraulic conductivities of the different components of the soil–plant continuum are all variable: xylem vessels of roots, stems, or leaves cavitate and lose conductivity at water potentials ranging from –1 to –8 MPa [18,19], and root conductivity (here referred to as the radial pathway) decreases with anatomical development due to suberization [20] and the formation of Casparian bands [21]; it can also reversibly change in a short time due to varying aquaporin (AQP) expression [22,23]; the root–soil interface has also a

variable hydraulic conductivity, which is expected to decrease as the roots shrink and lose contact with the soil [24]. Root hairs contribute to maintain the connection with the soil matrix [25], but they might also break due to increasing tensile force at low soil water potentials. The soil is arguably the region with the greatest loss in hydraulic conductivity and this loss strongly depends on soil types. Soil conductivity dramatically decreases in unsaturated water conditions due to the decrease in the cross-sectional area of water flow and a higher tortuosity of the flowpaths. One important characteristic of the soil hydraulic conductivity is that its change (increase or decrease) with water content is instantaneous. This means that, in contrast to other conductivity losses in the plant, such as embolism, soil conductivity is usually fully reversible upon rehydration. A remarkable exception to the reversibility of the soil conductivity is found in the rhizosphere, where root-secreted mucilage causes strong hysteresis in the rhizosphere hydraulic properties [26].

Figure 2A illustrates typical hydraulic conductivity curves of varying soil types and compares them with xylem conductivity curves from 40 deciduous and evergreen plant species [27]. In the typical range of soil water potentials (~0.02–1.5 MPa), xylem and soil conductivities differ by more than five orders of magnitude, with the soil conductivity dropping at less negative water potentials (units and definitions are discussed in Box 1 and SI2 in the supplemental information online). The large decrease of k_{soil} (cm s^{-1}) with decreasing soil water potential (MPa) and the radial geometry of the flow to a single root, with the flux density q (cm s^{-1}) increasing toward the root surface, cause the soil water potential to nonlinearly decrease toward the root surface. These

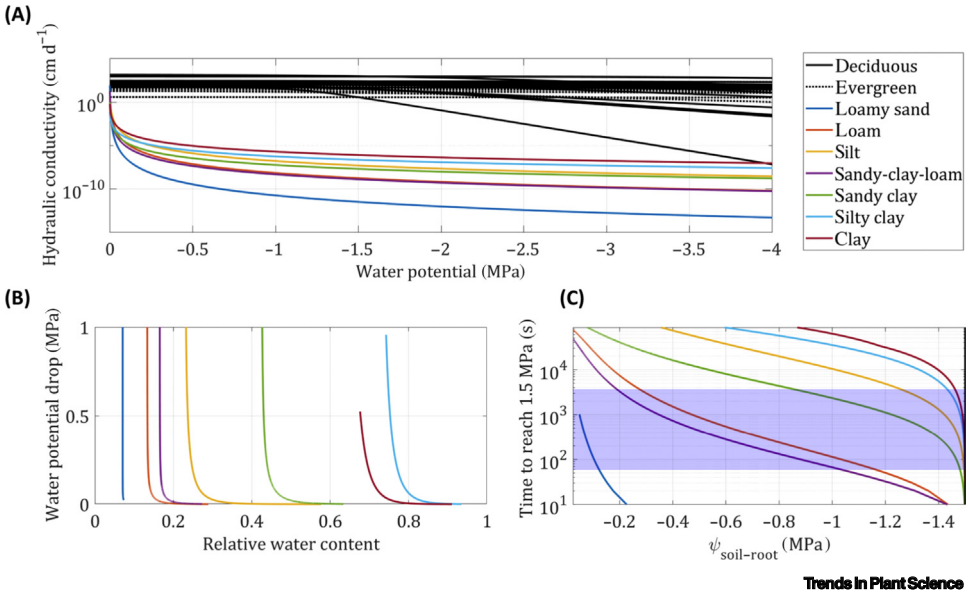

Figure 2. Soil Vulnerability Curves and Their Impact on Gradients in Soil Water Potential in the Rhizosphere. (A) Hydraulic conductivity curves from typical soils [51] compared with deciduous and evergreen xylem (specific) conductivity curves [27]. Xylem hydraulic conductivity is higher than soil hydraulic conductivity for typical soil water potential values. For more information, see SI2 in supplemental Information online. (B) Difference between bulk and root–soil interface water potential during a steady-rate uptake (7–10^{-7} cm d^{-1}) as a function of the relative saturation index for varying soils (see SI3 in the supplemental Information online for details). The water potential decrease between the bulk and soil–root interface increases dramatically at different saturation levels for each soil type. (C) Time needed to reach a water potential of –1.5 MPa at the soil–root interface as a function of the bulk soil water potential for a depletion rate of 0.006 cm^3 cm^{-3} d^{-1} for varying soils. The blue-shaded area spans the typical reaction time of stomata (between 1 min and 1 h). The loss of water potential at the soil–root interface is rapid and differs between soil types (see SI3 in the supplemental information online for details).

Box 1. Soil–Plant Hydraulic Model

We propose a simple model that provides the relation between potentials in soil, xylem, and leaves under steady-state assumption, when all fluxes should equalize between the bulk soil and the leaves. Other researchers have developed similar approaches to represent the soil–plant continuum (supply function) [1].

Water flow in the soil–plant system is driven by a gradient in water potential ψ (MPa), which depends on transpiration E ($m^3\ s^{-1}$) and is regulated by plant hydraulic conductance's (K_{root} and K_x) and soil hydraulic conductivity (k_{soil}) in series. Under steady-rate assumption, the radial soil water flux towards roots is represented by Equation I:

$$q = -\frac{k_{soil}(\psi_m)}{\rho g}\frac{\partial \psi}{\partial r}, \quad [I]$$

where q is the water flow rate at the root surface ($m\ s^{-1}$), ψ is the soil water potential (Pa), ρ is the water density, g is the gravitational acceleration, and r is the radial coordinate (m) [50]. The soil hydraulic conductivity k_{soil} ($m\ s^{-1}$) is a strongly nonlinear function of the soil matric potential ψ_m (Figure 1A in the main text). Assuming a uniform distribution of water uptake along the root system, q is related to transpiration E ($m^3\ s^{-1}$) according to Equation II:

$$q(r_0) = \frac{E}{2\pi r_0 L}, \quad [II]$$

where r_0 (m) is the root radius and L (m) is the length of the active roots. It follows that q decreases with increasing active root length. Using the Kirchhoff transformation, Equation I can be solved to find the water potential at the root soil interface ψ_{sr} for a given bulk soil matric potential ψ_{soil} (see SI1 in the supplemental information online).

In the root system, the flow equation is represented by Equation III:

$$E = -K_{root}(\psi_{x,r} - \psi_{sr}). \quad [III]$$

Equation III is solved to find the xylem water potential at the root collar $\psi_{x,r}$ given Kroot (m3 s–1 MPa–1), the root system hydraulic conductance. For simplicity, here we assume K_{root} to be constant, but this assumption can be easily replaced by a more complex relation, once this is known.

The flow equation in the xylem is represented by Equation IV:

$$E = -K_x(\psi)(\psi_{leaf} - \psi_{x,r}), \quad [IV]$$

where ψ_{leaf} is the leaf water potential and K_x ($m^3\ s^{-1}\ MPa^{-1}$) is the aboveground xylem conductance. Cavitation is included by describing the xylem conductance dependency to xylem water potential according to Equation V:

$$K_x(\psi) = K_{root}\left(\frac{\psi}{\psi_{0x}}\right)^{-\tau x}, \quad [V]$$

in which nonlimiting maximum xylem conductance is assumed. Equations IV and V using the flux matric potential approach (Equation S5 in the supplemental information online) yields ψ_{leaf}.

gradients can be calculated solving the equation of water flow toward the root surface [28] (Box 1). For a range of soil properties and for a typical soil water flux value of $7–10^{-7}$ cm s^{-1}, the drop in water potential from the bulk soil to the root surface is negligible in wet and conductive soils, but becomes increasingly steeper for decreasing water potentials (Figure 2B). Specifically, each soil type has a critical water potential (and relative water content) beyond which the water potential at the root–soil interface drops to very negative values much faster than the reaction time of stomata (i.e., between 1 min and 1 h [29,30]) (Figure 2C). The soil–root interface water potential at which this critical potential is reached in less than an hour largely varies across soils and ranges from –0.1 to –1.45 MPa. It follows that stomatal regulation that depends on a constant threshold value (e.g., –1.2 MPa) would fail to promptly protect plants against cavitation in most soils. Therefore, through evolution, plants must have developed efficient mechanisms to respond to this fast reduction by adapting their stomata regulation as a function of soil type.

Soil Hydraulic Limitation

Solving the equations of water flow across soil and plants (Box 1) gives the relationship between transpiration rate E ($cm^3\ s^{-1}$), bulk soil, and leaf water potentials ψ_{soil} (MPa) and ψ_{leaf} (MPa) (Figure 3A). Presenting the results as the surface $E(\psi_{soil}, \psi_{leaf})$ gives fundamental insights into soil and plant hydraulics and reconciles the views of plant physiologists (Figure 3C) and soil scientists (Figure 3B) on soil–plant water relations. The surface $E(\psi_{soil}, \psi_{leaf})$ represents the physically possible hydraulic states of the plant. When ψ_{soil} and ψ_{leaf} are equal, there is no gradient in water potential to drive water flow from the soil to the leaves and transpiration is null. When ψ_{soil} is high (i.e., in wet soil), increasing E results in a linear decrease in ψ_{leaf}. In wet soil, the surface starts to deviate from the linear relation only at high transpiration rates due to the decrease of xylem conductivity because of cavitation [8]. Whereas, as the soil dries out, the surface already starts to deviate from the linear relation at moderate transpiration rates because of the decreasing soil hydraulic conductivity. Xylem embolism determines the shape of $E(\psi_{soil}, \psi_{leaf})$ at high transpiration rates in wet soils, while belowground processes (namely rhizosphere hydraulic conductivity and root length) control its shape under dry conditions (examples shown in Figure S1 in the supplemental information online).

At any soil water potential, there is a critical E at which the surface deviates from the linear relation [16]. We define a stress onset limit (SOL), which divides the surface in two zones (red line in Figure 3A). The SOL (Box 2) is the point at which the slope of $E(\psi_{leaf}, \psi_{soil})$ at constant ψ_{soil}, $S_{leaf} = \left.\frac{\partial E}{\partial \psi_{leaf}}\right|_{\psi_{soil}}$, reaches 80% of its maximum value. In the linear zone (green zone in Figure 3A), neither the soil nor the xylem are subject to reductions in hydraulic conductivity. In the nonlinear zone (in brown in Figure 3A), the loss of xylem or rhizosphere hydraulic conductivity generates an additional resistance to flow causing a large drop in leaf water potential for a slight increase in transpiration rate. Note that the transition between the linear and nonlinear zones is continuous.

Figure 3 shows an exemplary surface and SOL in the (E, ψ_{soil}) and (E, ψ_{leaf}) planes. From the leaf perspective (Figure 3A), the SOL displays a similar shape to universal stomatal conductance responses of vascular plants [15,31]. From the soil perspective (Figure 3B), the SOL is consistent with well-accepted observations of nonlinear decreases of E with decreasing ψ_{soil} [32].

Given the marked nonlinearity of $E(\psi_{soil}, \psi_{leaf})$, an optimal strategy of plants undergoing soil drying is to promptly close the stomata while the SOL is approached [8]. To accomplish this function, stomata should be able to sense the change in leaf water potential in relation to a change in transpiration $\left(\frac{\partial \psi_{leaf}}{\partial E}\right)$. A mechanism that enables stomata to maintain plants in the linear zone of the hydraulic surface independently of environmental and soil conditions is not known and, thus is an outstanding question.

Experimental Evidence

The hydraulic surface $E(\psi_{soil}, \psi_{leaf})$ can be obtained from simultaneous measurements of leaf and soil water potentials and transpiration rate. An example with wheat (*Triticum aestivum* L.) is shown in Figure 4A, where the hydraulic model was fitted to accurate measurements obtained using a pressure chamber apparatus [33] (see parameters in Table S2 in the supplemental information online). In these experiments, the leaf xylem was maintained at atmospheric pressure, which affected the stomatal regulation and enabled plants to explore the nonlinear part of $E(\psi_{soil}, \psi_{leaf})$ without any xylem cavitation. In this example with pressurized plants, the loss of soil hydraulic conductivity alone caused the nonlinearity of the surface.

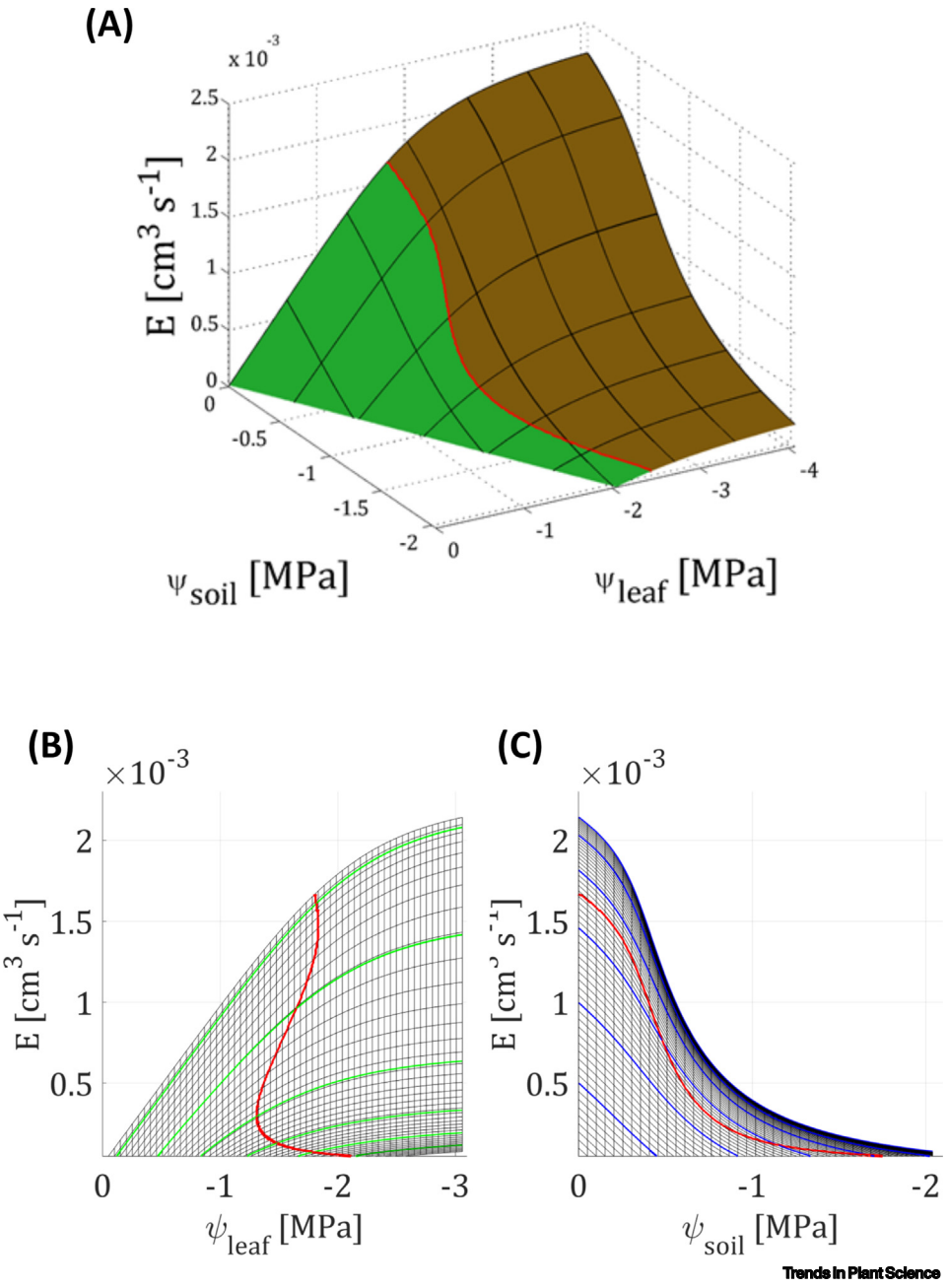

Figure 3. The Stress Onset Line (SOL) on the 3D Hydraulic Surface (A), from the Leaf (B), and from the Soil Perspective (C). (A) The 3D hydraulic surface is split into two zones by the stress onset line (SOL, in red). The transition between the linear (green) and nonlinear (brown) zones (shown as a thin red line) marks the onset of soil hydraulic nonlinearity and controls stomatal closure. (B) Exemplary transpiration E as a function of the leaf water potential ψ_{leaf} obtained from the hydraulic model. Green lines are iso-ψ_{soil}. As the soil dries, the slope of the iso-ψ_{soil} starts to decrease at lower E. The SOL (red line) is defined as the onset of the soil hydraulic limitation (see Box 2 in the main text) and we hypothesize that it shows the stomatal response to hydraulic limitation. (C) Transpiration E as a function of the soil water potential ψ_{soil}. Blue lines represent iso-ψ_{leaf}. The SOL (red line) shows the response of transpiration to soil drying. The early decrease in transpiration with soil water potential reflects the nonlinearity of the relation between ψ_{soil} and soil moisture. When plotted against soil moisture, E would remain relatively constant before dropping at low soil moisture levels.

Box 2. Onset of Soil Nonlinearity and Definition of a Critical Soil Water Potential ψ_{s50}

We define a limit (red trajectory in Figure 3A in the main text), which separates $E(\psi_{leaf})$ into linear and nonlinear parts: the SOL. For each soil water potential, we can calculate the slope of the iso-potential using Equation I:

$$S_{leaf}(\psi_{leaf}, \psi_{soil}) = \left.\frac{\partial E}{\partial \psi_{leaf}}\right|_{\psi_{soil}}. \quad [I]$$

The maximum of S_{leaf} occurs when $\psi_{leaf} = \psi_{soil}$ on the null-transpiration line and is called $S_{leaf,\,max}(\psi_{soil})$. The ratio between S_{leaf} and its maximum for a given ψ_{soil} represents the relative decrease S_{leaf}. We define a threshold beyond which we consider that the leaf water potential is decreasing significantly for a small increase of transpiration, as shown, for instance in Equation II:

$$\frac{S_{leaf}(\psi_{leaf}, \psi_{soil})}{S_{leaf,\,max}(\psi_{soil})} < 80\%. \quad [II]$$

Note that this 80% is arbitrary, but taking values ranging from 70% to 90% has little sensitivity on the SOL.

ψ_{H50} is defined as the maximum between ψ_{x50} and ψ_{s50}, where ψ_{s50} is the most negative soil matric potential at which up to 50% of the maximum transpiration E_{max} rate can be sustained. E_{max} corresponds to the transpiration rate when the stomatal conductance is maximal (not constrained by water stress). Assuming a radial geometry of the soil water flow, we calculate ψ_{s50} from the matric flux potential (Equation III):

$$\phi_{s50} = \frac{1}{2}\frac{E_{max}}{2\pi r_0 L}\left(\frac{r_0}{2} - r_0 r_b^2 \frac{\ln(r_b/r_0)}{r_b^2 - {r_0}^2}\right), \quad [III]$$

which is derived from Equation S3 in the supplemental information online, assuming that the soil matric potential at the root–soil interface is infinitely negative, so that the matric flux potential is null, and for 50% of E_{max}. ψ_{s50} is obtained from Equation III using the definition of the matric flux potential (Equation S2 in the supplemental information online). In doing so, we obtain the most negative soil matric potential at which $E_{max}/2$ can be sustained. ψ_{s50} is function of soil hydraulic conductivity, active root length, aboveground factors (e.g., leaf area and maximum stomatal conductance) and micrometeorological conditions (e.g., light intensity, vapor pressure deficit, and wind).

Detailed measurements of E and ψ_{leaf} in plants undergoing soil drying and exposed to varying transpiration rates [34] (red and blue open circles) show that stomata close at the onset of hydraulic nonlinearity and are well predicted by the hydraulic model that was fitted to the experimental data (SOL, red line) (Figure 4B). Figure 4B shows that stomata operate very close to the SOL, particularly in dry conditions and high vapor pressure deficit. Additional experimental evidence of the shape of the $E(\psi_{leaf})$ and its relation to k_{soil} has also been recently reported [31,35,36].

A large data set of experimental stomatal conductance functions from a meta-analysis on woody plants [37] further demonstrates that stomatal regulation maintains plants in the linear zone of $E(\psi_{soil}, \psi_{leaf})$. In Figure 4C, E is plotted as a function of $\Delta\psi = \psi_{soil} - \psi_{leaf}$. In the $(E, \Delta\psi)$ domain, the SOL is a straight line (Figure 4C, last subplot). Out of the 14 species for which data were available (Figure S3 in the supplemental information online), 11 show a significant linear trend with positive slopes (Table S2 in the supplemental information online). This remarkable result, given the potential uncertainty in the measurements and the multiple sources of data, demonstrates that stomata closure keeps plants in the linear zone of the hydraulic surface, confirming the hypothesis of Sperry and Love [16].

Soil versus Xylem Vulnerability

The current trend aiming to link transpiration to plant hydraulics is to consider xylem vulnerability as the primary hydraulic constraint to water flow. Consequently, emphasis is placed on the relation between ψ_{x50} (also referred to as P_{50}) and ψ_{gs50}. This relationship has been used to categorize stomatal strategies as risky or conservative [15,38]. A meta-analysis showed that, in

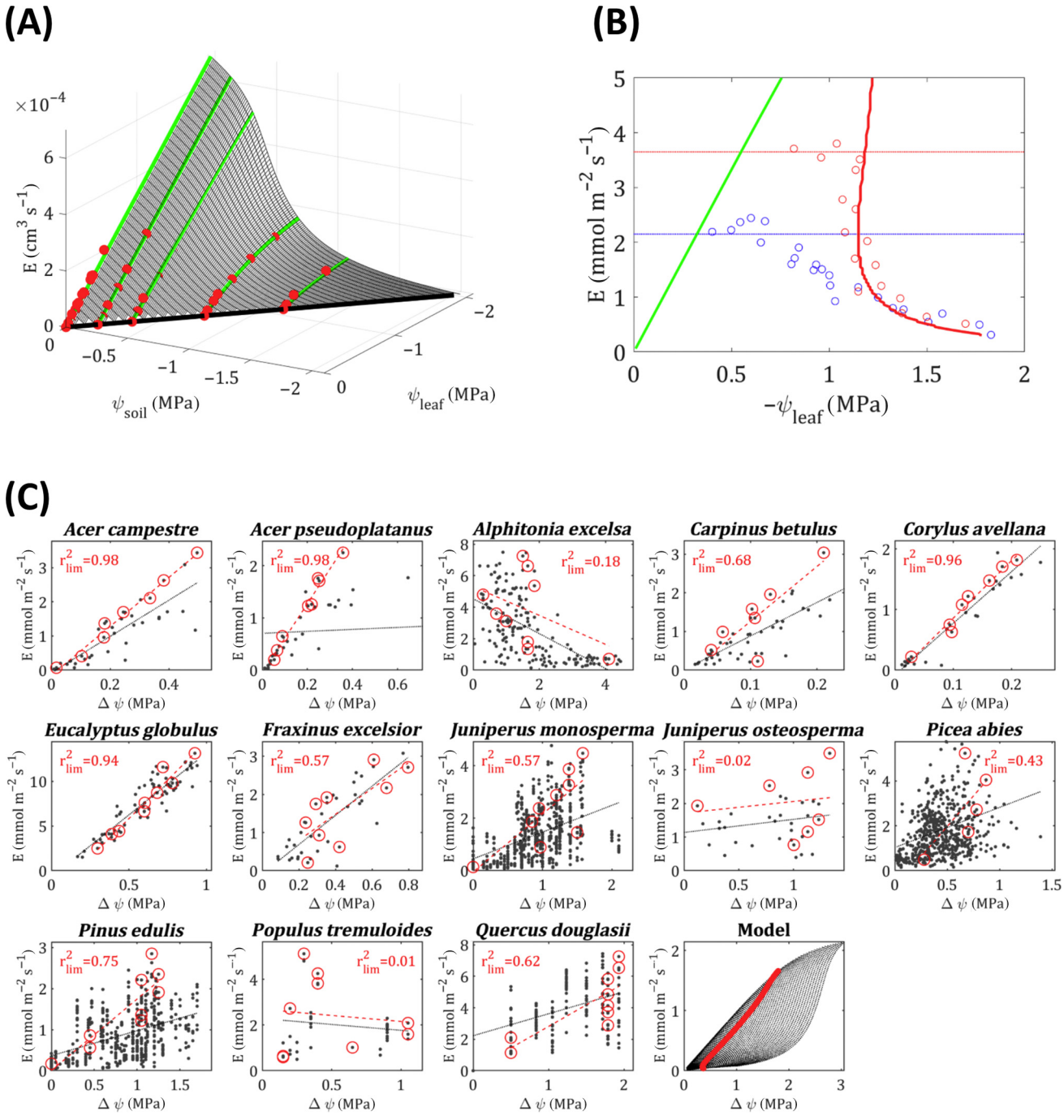

Figure 4. Experimental Evidence That Stomata Regulate Transpiration to Maintain a Linear Relation between Transpiration and Leaf Water Potential Loss. (A) Pressure chamber measurements [33] show the hydraulic relation $E(\psi_{soil}, \psi_{leaf})$. Red circles are measurements and green lines are iso-ψ_{soil} simulations (hydraulic parameters in detailed in Table S2 in the supplemental information online). The measurements were obtained by exposing the plant canopy to increasing light intensity and vapor pressure and measuring the suction in the leaf xylem. (B) Predicted transpiration reduction [stress onset line (SOL), red line] based on the hydraulic surface fits of the experimental decrease in E in soil drying experiments at high and low evaporative demands (red and blue open circles, respectively) [34]. The green line is the maximal boundary of $E(\psi_{leaf}, \psi_{soil}= 0)$ and its slope is equal to the plant hydraulic conductance. (C) Data from a meta-analysis of a broad range of woody species demonstrate that, at the frontier of stomatal closure, the relation between E and the difference between soil and leaf water potential (ψ) is linear for most species (dashed red lines), as predicted by our model (last subplot, SOL in red, other possible points on the hydraulic surface in black). r^2 is calculated on the data located at the stomatal closure frontier (see Figure S3 in the supplementary information online).

most cases, $\psi_{x50} < \psi_{gs50}$, which was interpreted as a conservative stomata response and which provides plants with a safety zone before cavitation occurs [15]. However, it is not clear how stomata could promptly react to a loss in xylem conductance much before a potential drop resulting from this conductance loss occurs. Additionally, this compromises the utility of hydraulic models to predict accurately transpiration responses to drought based on plant hydraulic traits.

An alternative interpretation is that the loss of soil hydraulic conductivity occurs at water potentials $>\psi_{x50}$. Using our model and letting the root length vary, we obtained curves that cover the experimental data (Figure 5A). For plants with short roots (violet line in Figure 5A) the water potential at the root–soil interface decreases at relatively high soil water potential and stomata close at relatively high water potentials ($\psi_{gs50} \approx -1$ MPa), no matter how negative is ψ_{x50}. For plants with longer roots (pink line in Figure 5A), the soil starts to limit the water supply to the roots at more negative water potentials, and ψ_{gs50} approaches ψ_{x50}. However, for plants with $\psi_{x50} < 3$ MPa, the soil remains the main hydraulic limitation. Indeed, at these water potentials, the soil hydraulic conductivity is so low that gradients in water potential inevitably occur across the rhizosphere. This exemplary calculations indicate that ψ_{x50} might not be sufficient to represent the loss of hydraulic conductivity of the soil–plant continuum and that including soil and root traits is needed to predict stomatal closure and its relation to soil–plant hydraulics.

Therefore, we introduce a new parameter, ψ_{H50}, to describe the onset of hydraulic limitation, including soil limitation. It is defined as the maximum between ψ_{x50} and ψ_{s50}, where ψ_{s50} is the lowest soil matric potential at which 50% of the potential transpiration can be sustained by soil water flow (Box 2). ψ_{s50} is a function of soil conductivity, root length active in water uptake, and potential transpiration. Plotting ψ_{H50} versus ψ_{gs50} gives a good match with the 1:1 line (Figure 5B), which means that stomatal closure corresponds to the point of soil hydraulic limitation. The new

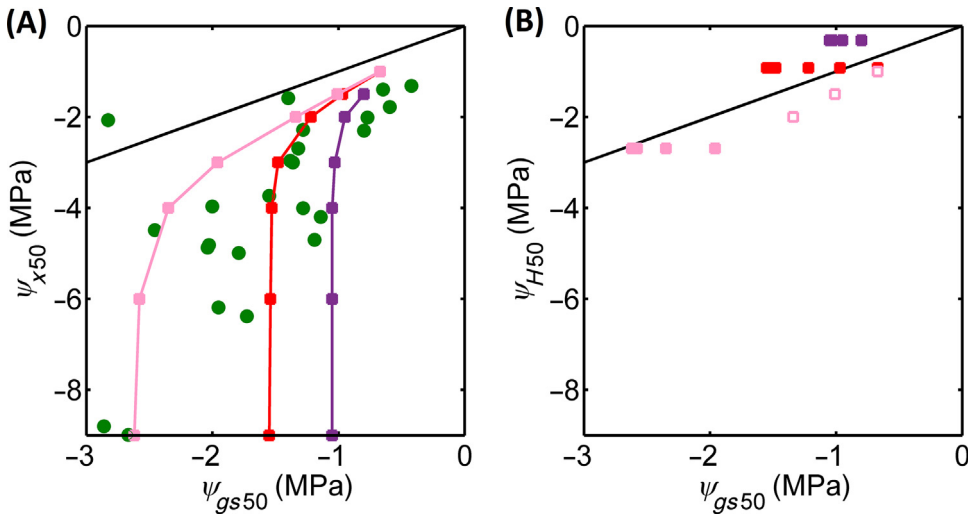

Figure 5. Soil (and Not Xylem) Loss of Conductance Is the Main Driver of Stomatal Closure. (A) Relationship between the water potentials ψ_{gs50} and ψ_{x50} at which stomatal and xylem conductance are 50% of their maximum value. Green circles are data across species [15]. Pink, red, and purple lines and solid squares are simulations with varying root lengths (pink L = 500 cm, red L = 2500 cm, and purple L = 12500 cm, other parameters in see Table S1 in the supplemental information online). The 1:1 line is shown in black. (B) Relationship between ψ_{gs50} and ψ_{H50}, where ψ_{H50} is the maximum between ψ_{x50} and ψ_{s50}, which is the lowest soil matric potential at which 50% of the potential transpiration can be sustained by soil water flow. Pink, red, and purple squares are the ψ_{H50} simulations with varying root lengths the ψ_{x50} of which is shown in (A). For the white-filled squares, $\psi_{H50} = \psi_{x50}$. The 1:1 line is shown in black.

defined parameter enables a more comprehensive analysis of hydraulic limitation and stomatal regulation.

Other plant tissues, such as leaves or roots, might also contribute to the drop in conductance of the whole soil–plant continuum. For instance, the leaf hydraulic conductance K_{leaf} drops during dehydration [39]. However, its contribution to whole-plant conductance might not be large, as recently shown in wheat [40].

Concluding Remarks

We have shown that soil hydraulic conductivity and root distribution are key to predicting and interpreting transpiration reductions during drought. Unlike xylem embolism, soil hydraulic conductivity is quickly reversible upon rehydration, allowing a rapid pressure transmission and increase in plant water potential when the soil rehydrates.

The newly introduced parameter ψ_{s50} helps synthesize belowground interactions into a concept linking soil drying to stomata regulation. However, predicting ψ_{s50} is challenging. Measuring soil hydraulic conductivity in the dry range and the fraction of roots adsorbing water is difficult. Equation III in Box 2 assumes a uniform uptake along the root length and a uniform soil water potential, which is rarely the case in the field. Functional-structural root–soil models, such as R-SWMS [41], are equipped to include nonuniform soil water potentials and root properties, but rely on several root parameters, such as the distribution of radial and axial hydraulic conductivities along the root system, which are not easily available. An additional complexity is that, during soil drying, roots might shrink and partly lose contact with the soil, with a consequent drop in the hydraulic conductivity of the soil–root system [24,42]. Recent measurements with olive plants showed the hydraulic conductivity of the root–soil interface severely dropped during soil drying and was the primary hydraulic limitation along the soil–plant continuum [31]. Therefore, including the dynamic properties of the root–soil interface appears crucial to properly understand belowground limitations, and ψ_{s50} might be less negative than its estimation based solely on soil hydraulic losses.

This novel view of the crucial role of soil conductivity on the onset of stomatal closure raises numerous questions (see Outstanding Questions). Therefore, phenotypic platforms, field trials, and meta-analyses that aim at characterizing stomatal responses to drought should consider soil hydraulic properties and root length to disentangle intrinsic plant properties from soil hydraulic constraints. According to the proposed approach, the same genotype grown in different soils is expected to have a different SOL and, thus, stomatal function. However, beside stomatal closure, plants have a broad range of belowground strategies to cope with soil hydraulic limitations. Plants continuously adapt their root architecture, anatomy, and hydraulic properties to the soil conditions through short and longer-term plastic responses: hydrotropism [43], hydropatterning [44], xerobranching [45], and aquaporin dynamics [46] attenuate the drop in soil hydraulic conductivity around roots. For instance, water stress-dependent circadian oscillations of root hydraulic conductance allow maize plants to anticipate and avoid the decrease of rhizosphere hydraulic conductivity [23,47]. By contrast, plants can also linearize the $E(\psi_{soil}, \psi_{leaf})$ surface by altering the hydraulic conductivity of the rhizosphere, for instance by growing root hairs [25,48] or exuding mucilage [49]. Coordination mechanisms between plant hydraulic status and longer-term growth have also been demonstrated. For instance, a decreased shoot:root ratio represents an ideal long-term adaptive mechanism to drought by decreasing E and increasing belowground conductance.

In summary, there is continuous crosstalk between stomatal regulation, leaf water potential, and soil–plant hydraulic conductance, which regulates plant development in relation to its

Outstanding Questions

What is the primary constraint on water flow in soil–plant systems? Simultaneous measurements of atmospheric conditions (light intensity and vapor pressure deficit), leaf water potential, and transpiration rates, coupled with measurements of xylem vulnerability, root architecture, and soil water potential distribution could reveal the relative importance of rhizosphere, root, and xylem vulnerability to the shape of the SOL.

What physiological mechanisms allow stomata to operate near the SOL? Is a stomatal model in which stomatal conductance is solely a function of leaf water potential sufficiently flexible to prevent plants from crossing the SOL for varying soil and atmospheric conditions? Does the relation between stomatal conductance and leaf water potential change with soil properties?

How does root conductance (in terms of active root length, root–soil contact and root conductivity) evolve with soil and plant water potential and what are the molecular mechanisms behind it? Do (and to what extent) roots adapt to soil drying by decreasing the gradients in water potential around the roots, for instance by growing root hairs, exuding mucilage, or hydropatterning? As roots shrink, they lose contact with the soil; what are the implications for the hydraulic conductance of the soil–plant continuum and on stomatal regulation?

To what extent does plant hydraulic capacitance impact plant water relations, hydraulic conductance, and the temporal dynamics of the relationship between transpiration, stomatal conductance, and leaf water potential?

The critical soil water potential ψ_{s50} is a function of soil hydraulic conductivity, active root length, aboveground factors (e.g., leaf area and maximum stomatal conductance), and micrometeorological conditions (e.g., light intensity, vapor pressure deficit, and wind): can ψ_{s50} be measured and compared with ψ_{gs50} and ψ_{x50}in soil-plant datasets?

environment. Our conceptual framework provides a sound basis to predict how transpiration regulation under drought evolves with plant development, including above- and belowground hydraulic traits.

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Supplemental Information

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