PLANT SCIENCE

Soils drive convergence in the regulation of vascular tension in land plants

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Terrestrial vascular plants operate under negative water potential, which results in hydraulic tension in the vascular system. Vascular tension varies with transpiration and soil drying and is regulated by stomata, pressure-activated valves on the leaf surface. We hypothesize that soil physical constraints drive convergence in the operational range of leaf vascular tension. Based on a meta analysis of 19 diverse species, we find that stomatal regulation of transpiration is activated when leaf vascular tension reaches a narrow target of 1.3 ± 0.6 megapascals. This value matches the range (1.4 ± 0.6 megapascals) predicted from an optimal soil water extraction model. Optimality in plant vascular tension appears to have evolved by selection for a narrow range of osmotic pressure in the leaves of diverse species growing across variable environments.

Carbon uptake for photosynthesis on land requires large quantities of water because of the dryness of the terrestrial atmosphere. Selection for productivity and growth has led most vascular plants to mine water from the soil, where it is transiently abundant. Extraction of soil water is achieved by the creation of a negative water potential at the evaporative surface of the leaf, which is transmitted as tension through the plant vascular system (xylem) into the soil where it draws water from soil pores. The combination of a water potential gradient in the vascular system plus cohesion between water molecules enables the flux of soil water upward into transpiring photosynthetic tissues, without the direct expenditure of metabolic energy (*1*). However, the costs associated with housing and maintaining water flow and growth increase as water potentials become more negative due to increased mechanical (*2*) and metabolic (*3*) demands on plant tissues. In addition, higher vascular tension also increases the risk of damage by xylem embolism (*4*). Balancing the benefits of a large water potential gradient between the soil and leaves, in terms of increased water extraction, against these costs appears to be a fundamental axis of tradeoff in the evolution of land plants (*5*, *6*).

The water potential in plants, ψ [Pa], consists of three components: pressure, gravitational potential, and osmotic potential. In the xylem, the effect of solutes (and osmosis) is negligible, leaving pressure potential and gravitation to drive water flow along the xylem. We refer to the negative pressure potential in the leaf xylem, $-\psi_{leaf}$, as leaf vascular tension, which increases as the xylem pressure potential becomes more negative during plant dehydration. The leaf xylem pressure potential covers a large fraction of the theoretical range of water potentials delimited by the soil and the atmosphere (Fig. 1A), above −0.1 MPa in wet soils and humid atmospheric conditions down to around −10 MPa in dry conditions for drought-tolerant species. But at these extremes, photosynthesis, transpiration, and growth are severely reduced. Herein lies a basic question in plant biology: What leaf vascular tension best enables plants to extract water from the soil?

Many attributes of plants contribute to determine the operational range of leaf vascular tension during fluctuations in atmospheric evaporative demand, including the ratios and efficiencies of tissues involved in water transport and gas exchange (*7*, *8*). However, one universal feature of vascular plants is the presence of pressure-activated stomatal valves on leaves, which exert overarching control on the rate of water use and hence the range of vascular tensions that exist in the xylem (*9*). Stomata also regulate CO_2 flow into leaves for photosynthesis and maintain a delicate balance between carbon acquisition and vascular tension associated with water loss. Stomata are dynamically regulated such that they can quickly adjust gas exchange in response to changes in atmospheric conditions, including light intensity, CO_2 concentrations, temperature, humidity, and internal leaf water status by means of interacting signaling pathways. Traditionally the action of stomata in regulating photosynthesis and water use efficiency has dominated efforts to model stomatal behavior, based on the assumption that plants optimize carbon gain over water transpired (*10*). However, during water limitation, the action of stomata, apparently guarding against excessive vascular tension in the plant, overrides stomatal control systems linked to photosynthetic gain (*11*). Today's plants are increasingly exposed to atmospheric dryness (*12*, *13*) and soil water deficit (*14*), motivating our goal to explain and predict this poorly understood tension-regulating aspect of stomatal control.

One modeling approach of stomatal regulation stipulates that stomata optimize carbon gain over a water cost, which has been differently defined. The original concept, which assumes that plants optimize carbon gain over water use (*10*), has been further elaborated to assign a cost to water that is related to the risk of cavitation and loss of hydraulic functions (*15*). By definition, these models predict that stomata should close before vascular tension reaches levels that would trigger xylem embolism formation (*15*–*17*). Although the order of these events (first stomatal closure and then embolism) provides a well-established safety margin for plants during drought (*6*), there is substantial variability and uncoupling between these vascular tension thresholds (*18*). Seeking a general explanation for the regulatory target of vascular tension and for how stomatal optimality might be reached, our objectives here are: (i) to evaluate the range of vascular tensions that trigger stomatal regulation of transpiration in diverse species; (ii) to understand what process delimits this range; and (iii) to propose a likely mechanistic feature upon which selection could act to constrain the range of vascular tension range in the leaf.

We first sought to characterize the range of vascular tensions observed to activate stomatal regulation of transpiration during incipient water deficit. We posit that under dehydrating conditions, the initial closing action of stomatal valves to limit increasing vascular tension should provide a clear indication of the target range for pressure control in plants. To disentangle tension-related stomatal behavior from stomatal responses to photosynthetic rate, we use metadata of stomatal response to drying soil that exclusively considers behavior under non–energy-limiting conditions. We targeted the critical tension at which stomata start closing (critical tension at ~10% stomatal closure: $-\psi_{gs,crit}$) to indicate the incipient regulation point while plants were still undertaking near steady-state extraction and transport of water from the soil to the leaves. Understanding the magnitude and range of this regulatory threshold allowed us to determine whether this critical regulatory point is conserved or variable across species and soils.

A convergent target in the regulation of vascular tension

Our analysis of existing metadata of plant water relations across diverse species and biomes (*19*) shows that the critical leaf vascular tension at which transpiration starts to decline, $-\psi_{gs,crit}$, occurs within a narrow range (Fig. 1, B and C): $-\psi_{gs,crit} = 1.3 \pm 0.6$ MPa (mean and standard

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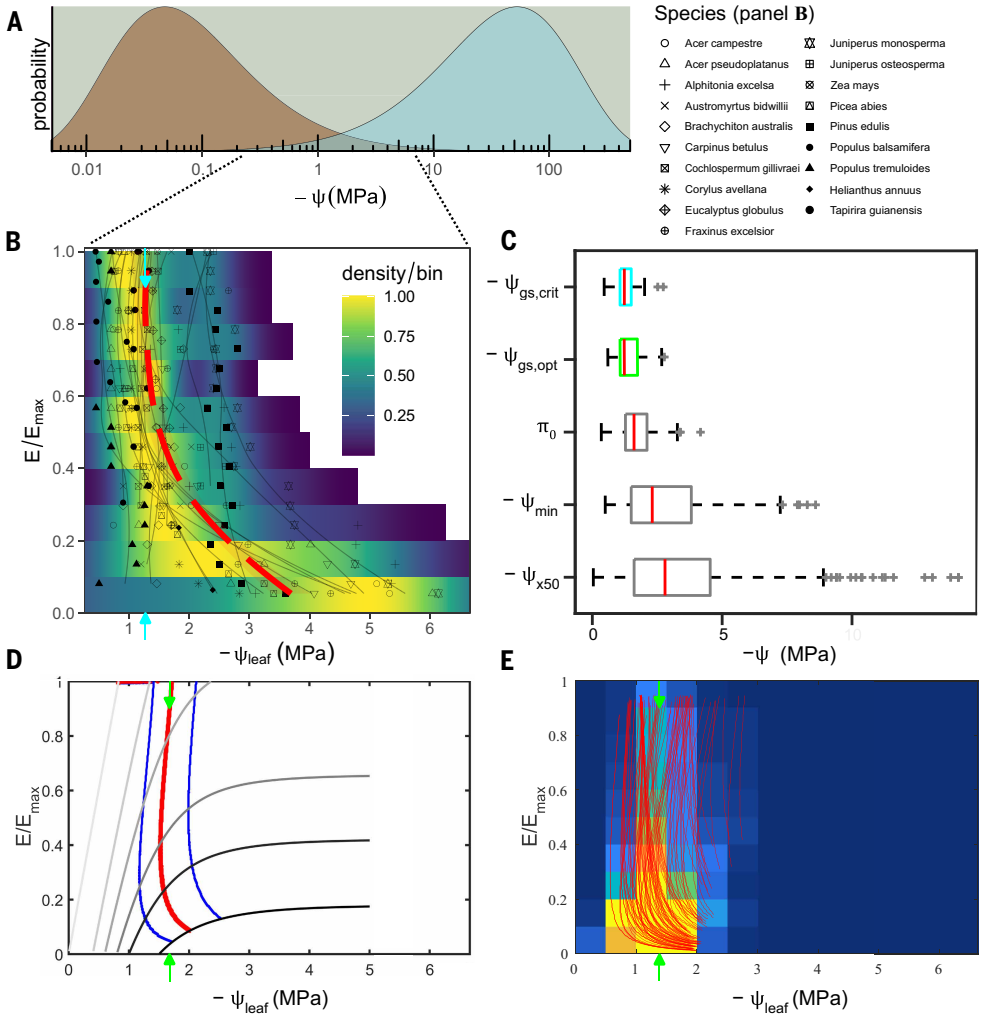

Fig. 1. A Plant water potential [ψ (MPa)] spanning several orders of magnitude depending on the water potential. (**A**) Water potential of soils and atmosphere is indicated by brown and blue, respectively; water existing at a given water potential is represented as probability density. (**B**) Measured reduction in relative transpiration rate (E/E_{max}) with increasing leaf vascular tension ($-\psi_{leaf}$) for 17 diverse tree species (*19*) and two representative crops (*9*). The dashed red line and shading show local polynomial regression and standard error across all species together with a normalized heatmap showing the probability density per transpiration bin (blue-yellow). Species-specific transpiration down-regulation (see top right corner for species legend) is indicated by solid black lines and symbols. The leaf vascular tension at which stomata start to close is calculated as ~10% stomatal closure ($-\psi_{gs,crit}$) for each species (the average value is indicated by the cyan arrow). (**C**) Box plots of observed and predicted leaf vascular tensions across species and environments [medians in red, ranges (25th and 75th percentile) are given by box edges, extreme data indicated by whiskers and outliers indicated by plus sign markers]: $-\psi_{gs,crit}$ shows incipient stomatal closure derived from data in (B); $-\psi_{gs,opt}$ is the simulated optimum leaf vascular tension at the onset of stomatal down-regulation (~10% closure) for varying plant hydraulic conductance, root length, xylem vulnerability and soil properties ($n = 108$); π_o is the mean bulk leaf osmotic pressure for $n = 302$ diverse woody species (*26*); $-\psi_{min}$ and $-\psi_{x50}$ are the seasonally highest vascular tensions experienced by plants ($n = 223$ species) and the vascular tension at 50% loss of stem xylem conductance ($n = 480$ species), respectively (*20*). (**D**) Exemplary simulation of declining transpiration in response to increasing leaf vascular tension during soil drying: from light gray ($-\psi_{soil} = 0.01$ MPa) to black ($-\psi_{soil} = 1$ MPa), each line refers to a soil water potential for an average plant in a loamy soil. The onset of hydraulic nonlinearity [i.e., $\frac{\partial E}{\partial(-\psi_{leaf})}$ is 0.5 of its maximum] is indicated in red (blue for 0.25 and 0.75 of the maximum). The critical leaf vascular tension when stomata should start to close (10% closure) is indicated by the green arrow ($\psi_{gs,opt}$). (**E**) Heatmap of onsets of nonlinearity for varying plant traits (27 sets of parameters) in sandy loam, loam, sandy clay loam, and clay loam, with the mean $-\psi_{gs,opt}$ indicated by the green arrow.

deviation from 17 trees and two crops; median = 1.2 MPa). Trees and crops exhibit similar behavior, independently of whether they are considered isohydric [i.e., having a stringent stomatal closure, e.g., *Zea mays* L. (maize)] or anisohydric [i.e., having a less stringent stomatal regulation, e.g., *Helianthus annuus* L. (sunflower)] (*9*). This tight target range for leaf vascular tension regulation contrasts with the broad range of tensions (Fig. 1C) that plants can experience and tolerate under drought conditions (*20*). In fact, the largest tensions (most negative water potential) recorded in field plants ($-\psi_{min}$) reach values up to 8.6 MPa, whereas the tensions required for 50% embolism in the vascular systems of plant species ($-\psi_{x50}$) range from near 1 MPa in sensitive rainforest species to beyond 10 MPa regularly in arid zone specialists (*6*), with a record of 19 MPa (*21*) in a resilient conifer species.

When viewed in the light of our observation here of convergence in $-\psi_{gs,crit}$, this large range of tolerances make it unlikely that protection from xylem embolism is the proximate explanation for the activation of stomatal regulation of leaf vascular tension during drying. It has been alternatively suggested that other types of tension-induced vascular dysfunction in leaves (*22*) and roots (*23*) might provide an explanation for protective stomatal closure at increasing tension, but none of these provide any evidence for intrinsic physiological limitations in function of these tissues that might explain the narrow target we observe here.

Soil hydraulics constrain the upper limit of the optimal plant vascular tension range

Most of the water used by vascular plants is stored in the soil. The flow of soil water to the root surface becomes increasingly difficult as soil water content decreases, its tension increases, and the ability of the soil to conduct water (hydraulic conductivity) drops (*24*). The critical thresholds at which soil water supply becomes limiting are a function of soil pore size distribution and vary with soil texture (*25*). We propose that evolution has led plants to converge upon a narrow range of leaf vascular tension threshold, $-\psi_{gs,crit}$, because this achieves an optimal rate of water extraction relative to cost (in terms of elevated vascular tension) applied across a broad range of plant hydraulic traits and soil types. This idea was tested using a hydraulic model that represents water flow from the soil to plant as a bulk flow pathway driven by the tension gradient from the soil to the leaf for varying plant and soil properties. We assumed a steady-state water extraction from soils (i.e., that the contribution to transpiration of plant-stored water is minimal).

Solving the water flow equations (eq. 1 to 3 in methods) demonstrates that extraction of soil water by roots generates a highly nonlinear increase of the soil water tension toward the roots, and when tension starts to rise it leads to a feedback in hydraulic tension (*24*) which then propagates

along the vascular system to the leaf xylem. As soils dry, the volumetric fraction and radius of water-filled pores decline and thus the water tension at the root-soil interface and along the vascular system must further increase to sustain the transpiration demand. But in doing so, the soil hydraulic conductivity drops as well which requires even more tension to extract water, in a feedback loop, which leads to a maximum flow rate that can be sustained (the flow rate at which the gray lines reach a plateau in Fig. 1D). This implies that for a given soil-plant system at a certain bulk soil water content $\frac{\partial E}{\partial(-\psi_{leaf})}$ decreases toward zero (where E is the transpiration rate). A decline in $\frac{\partial E}{\partial(-\psi_{leaf})}$ means a decreasing efficiency in soil water extraction; physically speaking, the water potential is related to the work to extract water and $\frac{\partial E}{\partial(-\psi_{leaf})}$ quantifies the increase in water extraction rate per increase in this work. We stipulated a 50% reduction in $\frac{\partial E}{\partial(-\psi_{leaf})}$ to define a limit to the efficiency in soil water extraction (note that similar values are yielded using thresholds of 25 and 75%, Fig. 1D). Beyond these thresholds, water uptake from the soil rapidly becomes suboptimal in terms of water yield per vascular tension increment.

Applying our hydraulic model using 27 combination of plant traits (plant hydraulic conductance K_{plant}, active root length L_{root}, and ψ_{x50}) in the four most commonly occurring soil textural classes (sandy loam, loam, sandy clay loam, and clay loam, which cover most vegetated land), we found that the leaf vascular tension before water uptake becomes inefficient $\left(\text{i.e., 50\% reduction in } \frac{\partial E}{\partial(-\psi_{leaf})}\right)$ is in a narrow range ($-\psi_{gs,opt}$ =1.4 ± 0.6 MPa, median 1.1 MPa) that matches well with the observed $-\psi_{gs,crit}$. We conclude that the strict soil hydraulic limit to efficient water uptake has constrained vascular plants to converge toward the $-\psi_{gs,crit}$ value we observed, ~1.3 MPa.

Plants should be able to target efficiency in the physical aspects of soil water extraction through the behavior of their stomata, but such a target is only optimal in an evolutionary sense when considered in terms of specific cost and benefit functions (*10*). Our physical definition $\left[\frac{\partial E}{\partial(-\psi_{leaf})} \text{ remaining above 50\% of its maximum}\right]$ is related to stomatal optimality mainly through its impact on the cost of opening stomata. Leaf vascular tension ($-\psi_{leaf}$) is linked to a cost function in terms of the additional material (thickening) reinforcement of the xylem required to support the collapsing force of tension in the xylem (*2*). Added to this is the increasing cost of maintaining osmotic gradients in the living tissues of the plant to maintain functionality as xylem tension increases (*3*). Furthermore, increasing vascular tension imposes an increased operational risk in terms of xylem cavitation damage, which appears largely irreversible (*4*). "Benefit" in our definition is expressed in terms of increasing soil water extraction for transpiration. Although transpiration is not a direct benefit to the plant, transpiration is tightly linked to assimilation (the most likely candidate to serve as the benefit) through the common diffusive pathway for vapor and CO_2 through the stomatal pore. More soil water extracted per unit of time allows for higher E, implying higher assimilation rate. The shape of the relation $E(\psi_{leaf})$ (for any given soil water potential) is such that once the slope $\frac{\partial E}{\partial(-\psi_{leaf})}$ starts to decline in drying soil, it rapidly approaches zero in a small range of leaf water potential (Fig. 1D). This decline implies that the cost of water (as determined by vascular tension) would keep increasing toward infinity, while the increase in benefit (e.g., assimilation) would be marginal. Because of the steep increase in the cost of water once $\frac{\partial E}{\partial(-\psi_{leaf})}$ begins to fall, maintaining stomata open beyond $\psi_{gs,crit}$ is suboptimal. In summary, our definition $\psi_{gs,crit}$ sets an upper boundary for stomatal optimality.

Osmotic potential as a selection target

Having shown that the physical constraints on soil water extraction can explain why plants converge upon a common target for stomatal regulation of vascular tension, we hypothesize that the mechanism for this convergence lies in evolutionary selection for a narrow range of cellular osmotic pressure (π_o) in the leaf mesophyll of plant species. Indeed, this is exactly what is observed from meta analyses of bulk leaf π_o from diverse species and habitats (*26*), which show a narrow range (Fig. 1C), centered at −1.6 MPa (25th and 75th percentile of more than 200 species being −1.28 and −2.11 MPa). Such a narrow range of π_o would lead to convergent stomatal regulation of vascular tension among species because π_o determines mesophyll cell turgor pressure, which in turn regulates production of the primary stomata-closing hormone abscisic acid (ABA). Maximum mesophyll turgor pressure is determined by π_o, yet this pressure declines directly with the total water potential during dehydration, triggering ABA production and stomatal closure as mesophyll turgor approaches zero (*27*, *28*). Applying a standard correction for solute dilution (*29*), the observed median π_o of −1.6 MPa translates to mesophyll turgor loss at a water potential of −2.0 MPa. This value is 0.6 to 0.7 MPa more negative than the optimal leaf xylem pressure potential predicted by our model and the convergent $\psi_{gs,crit}$ observed in diverse species. This difference is close to the value expected due to hydraulic gradients between the xylem and mesophyll cells in the leaf (*30*, *31*). The narrow range of π_o and its consistency with both, $-\psi_{gs,opt}$ and $-\psi_{gs,crit}$, provides support for our hypothesis connecting evolutionary pressure to optimize water extraction from soils with a mechanistic target for selection in the leaf.

Discussion

We present an explanation for the convergence in the regulation of leaf vascular tension in land plants. This convergence is identified as a narrow range of $-\psi_{gs,crit}$ responsible for activating the stomatal regulation of transpiration across a sample of diverse species. A soil-plant physical model explains how this behavior prevents plants from operating suboptimally in terms of soil water extraction. However, additional processes are required to satisfy formal optimality in stomatal regulation under variable environmental conditions, which involves assimilation as first target instead of transpiration and which requires additional mechanisms to respond optimally to environmental perturbations such as changes in light, temperature, humidity, and CO_2 concentration.

The convergence in leaf osmotic potential driven by soil physical constraints, besides explaining stomatal response to soil water deficit, also explains stomatal response to evaporative demand under conditions of nonlimiting soil conductivity. In wet soils it is the hydraulic conductance of the plant that largely dictates leaf vascular tension during transpiration. As a result, rises in transpiration rates caused by increasing vapor pressure deficit could be sufficient to cause ψ_{leaf} to approach π_o, triggering stomatal closure via the same mechanism as during soil drying. Thus, we posit that the observation of a general stomatal response to vapor pressure deficit in wet soils (*32*) is consistent with a conservative π_o, evolved under the constraints of soil physics, and mediated by the ratio of hydraulic and diffusive conductances in the roots, stems, and leaves of plants (*33*, *34*).

Our results suggest rather conservative stomatal behavior, whereas other studies have emphasized diversity among species in stomatal response (*35*). The distinction here is that we focus on the action of stomata under typical (nondrought) conditions of near steady-state gas exchange and vascular tension, in which the bulk of transpired water is immediately derived from the soil rather than plant water stores. Limiting our study to these mild stress conditions, in which the vast bulk of terrestrial plant gas exchange takes place, revealed a hydraulic set-point for stomatal regulation at a leaf vascular tension around 1.3 MPa. This value closely matches predictions based on principles of water flow in unsaturated porous media and the concept that plants optimize their exposure to vascular pressure during water extraction from the soil.

By contrast, studies emphasizing the diversity of stomatal behavior and its correlation with xylem vulnerability focus on the survival phase of plant drought response, when transpiration is reduced to a small fraction of its potential maximum and when transpiration increasingly depends on plant internal water storage. The imposition of severe water

deficit appears to drive divergence between species in stomatal behavior during the survival phase of drought (*36*, *37*). This divergence among plant species is an expected product of tradeoffs in the cost and benefit of traits linked to plant survival, such as xylem resistance to cavitation and water storage (*38*). Interactions between plant functional traits and the environment permit the coexistence of diversity in the way stomata of different species manage water use in the final stages of drought, when stored water becomes a major component of the transpired water (*39*). This highlights the importance, when describing stomatal dynamics, of distinguishing the early stomatal closure we associate here with the maintenance of optimal water extraction from soils, from later stages of stomatal closure required for plant survival during drought.

The convergent optimal leaf vascular tension identified here provides a likely explanation for other linkages in the evolution of land plants. Primary among these is the observed coordination between the efficiency of vascular transport in plant tissues and the gas exchange capacity of land plant species (*7*, *8*, *40*), which can only be explained if the tension used by plants to extract water from soils is constrained to a narrow range. The soil physical model used here provides a first-principles explanation of why, despite the huge range of plant morphology, photosynthetic physiology, temperature, atmospheric vapor pressure, and soil types, vascular tension during maximal photosynthesis in land plants remains within narrow boundaries. Mangroves provide an exception to prove the rule; existing in an environment where the water source does not conform to the porous media limitations relevant for soils, appears to have freed them to operate across a larger range of target leaf vascular tensions (*41*).

Other features such as maximum tree height may also be linked to convergence in the operating leaf vascular tension range in plants. Gravitational potential dictates that the vascular tension at the top of the tallest trees (around 130 m) will be 1.3 MPa even in wet soil and without transpiration. This value converges upon the vascular tension range where our model and observations would predict stomatal closure should be initiated (not factoring the additional impact of gravitational force). Without substantial leaf osmotic adjustment, this would result in stomata remaining increasingly closed during the day, severely limiting photosynthesis as maximum tree height is approached (130 m). Previous studies have postulated that the maximum height of coastal redwoods is limited by the osmotic potential of leaves (*42*), but without providing an explanation for why this osmotic limit might exist. We provide such an explanation, using hydraulic theory to account for an operational limit in osmotic potential which is ultimately constrained by soil properties. One might question why tall trees do not simply concentrate solutes in leaves to overcome gravitational limitation. We posit that there will be strong selective pressure to constrain variation and plasticity in π_o. Although an enhanced π_o may enable stomata to remain open at higher tensions, the cost of maintaining significant transpiration while soils cannot supply water at steady state will be a lethal failure of vascular function as drying progresses. For this reason, we expect that under most conditions, variation in π_o is selected against. The narrow target for optimality in hydraulic tension is not only supported by the small range of π_o observed among diverse plants but also by the fact that despite intense interest, crop genotypes with enhanced π_o show little improvement in growth under water deficit conditions (*43*, *44*).

Explanations for stomatal behavior as soils dry have covered a lot of ground in the last century or so since Francis Darwin invented tools to measure vapor fluxes from leaves. Our evidence suggests that soil physical constraints drive convergence in the range of operational vascular pressure in plants and that this is realized by selection for a narrow target in π_o across diverse species and environments.

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SUPPLEMENTARY MATERIALS

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Editor's summary

Plants transport columns of water through the vasculature to leaves under tension. Looking across diverse species inhabiting varying environments, Carminati *et al*. established that there is a narrow range of leaf vascular tension thresholds at which transpiration starts to decline. Using a theoretical model, the authors found that this convergence in leaf vascular tension threshold can be explained by the physical constraints of soil properties on water extraction by roots. Large pockets of water are easily drained, but as these diminish in size, capillary and viscous forces increase, making water challenging to extract. The greater vascular tension required to extract water from drier soils makes transpiration physically inefficient. This concept explains universal constraints on plant water relations. —Madeleine Seale

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