Pragmatic hydraulic theory predicts stomatal responses to climatic water deficits

John S. Sperry¹, Yujie Wang¹, Brett T. Wolfe², D. Scott Mackay³, William R. L. Anderegg¹, Nate G. McDowell⁴ and William T. Pockman⁵

¹Department of Biology, University of Utah, Salt Lake City, UT 84112, USA; ²Smithsonian Tropical Research Institute, PO Box 0843-03092, Balboa, Panama; ³Department of Geography, State University of New York, Buffalo, NY 14260, USA; ⁴Earth and Environmental Sciences Division, Los Alamos National Lab, Los Alamos, NM 87545, USA; ⁵Biology Department, University of New Mexico, Albuquerque, NM 87131, USA

Summary

• Ecosystem models have difficulty predicting plant drought responses, partially from uncertainty in the stomatal response to water deficits in soil and atmosphere. We evaluate a ‘supply–demand’ theory for water-limited stomatal behavior that avoids the typical scaffold of empirical response functions. The premise is that canopy water demand is regulated in proportion to threat to supply posed by xylem cavitation and soil drying.

• The theory was implemented in a trait-based soil–plant–atmosphere model. The model predicted canopy transpiration (E), canopy diffusive conductance (G), and canopy xylem pressure (P_canopy) from soil water potential (P_soil) and vapor pressure deficit (D).

• Modeled responses to D and P_soil were consistent with empirical response functions, but controlling parameters were hydraulic traits rather than coefficients. Maximum hydraulic and diffusive conductances and vulnerability to loss in hydraulic conductance dictated stomatal sensitivity and hence the iso- to anisohydric spectrum of regulation. The model matched wide fluctuations in G and P_canopy across nine data sets from seasonally dry tropical forest and pinyon–juniper woodland with < 26% mean error.

• Promising initial performance suggests the theory could be useful in improving ecosystem models. Better understanding of the variation in hydraulic properties along the root–stem–leaf continuum will simplify parameterization.

Introduction

Stomatal pores control rates of terrestrial photosynthesis and transpiration, particularly under water-limited conditions. Partial or complete stomatal closure reduces plant water stress, but at the cost of reduced productivity, elevated heat, light, and pest stress, leaf shedding, and mortality. Climate change is predicted to cause more frequent and intense droughts in many regions (Dai, 2011), yet current ecosystem models poorly capture observed drought responses (Allen et al., 2010; Powell et al., 2013). It is important to have an accurate and efficient way of predicting stomatal responses to water deficits if we are to improve our poor ability to model responses to drought. The stimulus–response pathways that underlie stomatal adjustments are not fully understood at the mechanistic and molecular levels (Buckley & Mott, 2013). But we can still predict stomatal behavior from its emergent properties. In this paper, we evaluate a theory of water-limited stomatal regulation that is based on the balance of water supply and demand (Sperry & Love, 2015).

As soon as John Milburn began listening to acoustic emissions from xylem cavitation, the implications for stomatal regulation were recognized (Milburn, 1973, 1979). It has become accepted that stomatal closure in response to water deficits in soil and atmosphere is associated with protecting the xylem from excessive cavitation (Field & Holbrook, 1989; Sparks & Black, 1999; Tombesi et al., 2015). Supply–demand theory formalizes this concept (Sperry & Love, 2015).

On the supply side, the transpiration stream is delivered to the leaves by the cohesion–tension mechanism (Pickard, 1981; Brown, 2013). This physical process is directly coupled to soil and atmospheric water deficits (Fig. 1a). Soil dryness dictates the upstream water pressure for the transpiration stream. Atmospheric dryness determines the potential rate of flow and the downstream pressure. More negative pressures increase flow resistance by causing cavitation in xylem conduits, and draining of soil pores in the rhizosphere (Fig. 1b). The dangerous feedback between falling pressure and rising flow resistance has been modeled for many years (Tyree & Sperry, 1988; Jones & Sutherland, 1991; Sperry et al., 1998) and is referred to as a vascular ‘supply function’ (Fig. 1c; Sperry & Love, 2015).

The supply function is the steady-state relationship between rising transpiration rate (E) and consequently falling canopy

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The supply–demand model. (a) A conductance network links layers of bulk soil ($P_{\text{soil}}$ = soil water potential) via rhizosphere and root paths to the stem and leaves. (b) Each network component has a vulnerability curve (VC) describing its drop in hydraulic conductance ($k$) with more negative pressure ($P$). (c) Integrating network vulnerability curves across the pressure drop from $P_{\text{soil}}$ to $P_{\text{canopy}}$ yields a vascular supply function: steady-state transpiration rate ($E$) vs $P_{\text{canopy}}$. These functions rise from a predawn $P_{\text{canopy}}$ at $E = 0$ to $E_{\text{crit}}$ (at corresponding $P_{\text{crit}}$). The $dE/dP$ derivative (dashed tangent) reflects the canopy hydraulic conductance, which goes to zero at the $E_{\text{crit}}$ hydraulic limit. As soil dries out, the predawn intercept (closed circles) becomes more negative and $E_{\text{crit}}$ (open circles) drops. (d) A demand function derived from the supply function determines the stomatal regulation of $E$ in response to drier air (which pushes the plant up its supply function) and dry soil (which shrinks the supply function). The demand function yields a physiological ‘demand limit’ that saturates $E$ below $E_{\text{crit}}$.

xylem pressure ($P_{\text{canopy}}$) for constant soil water potential (Fig. 1c, curves rising from predawn $P_{\text{canopy}}$ symbol). The supply function can be calculated by integrating ‘vulnerability curves’ that describe the loss of hydraulic conductance with negative pressure (Fig. 1b, ‘VCs’; Sperry & Love, 2015). The derivative of the supply function, $dE/dP_{\text{canopy}}$ (Fig. 1c, dashed $dE/dP$ tangent), is proportional to the hydraulic conductance at the canopy end of the flow path. The $dE/dP_{\text{canopy}}$ falls to zero beyond a maximum $E$ (Fig. 1c, $E_{\text{crit}}$ symbol) as cavitation increases and blocks flow. Drier soil truncates the supply function and diminishes $E_{\text{crit}}$ ultimately to zero (Fig. 1c, ‘drier soil’ arrow). The supply function extends to lower pressures when the xylem is more resistant to cavitation and when there is greater root surface area to minimize resistance to flow across the rhizosphere (Sperry et al., 1998, 2002a).

On the transpiration demand side, the theory proposes a ‘stomatal demand function’ (the ‘loss function’ of Sperry & Love, 2015) that locates the plant on its shifting supply function (Fig. 1d). The demand function represents the emergent coordination between leaf water supply and atmospheric water demand as limited by stomatal regulation. Stomatal regulation of $E$ should not allow $E_{\text{crit}}$ to be exceeded because this would prematurely desiccate the canopy and leave usable water in the soil. Even approaching $E_{\text{crit}}$ is risky, because the accelerating decline in $dE/dP_{\text{canopy}}$ increases the cavitation consequences of minor $E$ fluctuations. Nevertheless, the plant should exploit its ability to extract soil water and sustain $E$ as far into a soil drought as $E_{\text{crit}}$ permits. The demand function explained in Sperry & Love (2015) (their fig. 2) has stomatal closure reducing $P_{\text{canopy}}$ in proportion to the loss of canopy hydraulic conductance (quantified by the decline in $dE/dP_{\text{canopy}}$) that would occur without closure. The more environmental conditions threaten the pipeline, the greater the protective response. The result is a physiological limit to the stomatal demand that keeps $E$ safely below the $E_{\text{crit}}$ limit regardless of the dryness of soil or air (Fig. 1d, ‘demand limit’ curve). The system only fails hydraulically if the predawn $P_{\text{canopy}}$ drops enough to drive $E_{\text{crit}}$ to zero.

The supply–demand theory occupies a unique place among attempts to model stomatal behavior. It is not a mechanistic model of stimulus–response control at the molecular or physiological scale (Tardieu & Davies, 1993; Li et al., 2006; Buckley & Mott, 2013; Franks, 2013). It is not an empirical model with coefficients divorced from physiological process (Jarvis, 1976; Ball et al., 1987; Stewart, 1988; Lloyd, 1991; Leuning, 1995). Although it is based on an adaptive, emergent property of stomata (the balance of water demand with limited supply), it is not an optimization model like that of Cowan (Cowan, 1977; Medlyn et al., 2011), which is based on an unknown variable ($\lambda$, the marginal carbon cost of water loss). Models that assume a near-isohydric $P_{\text{canopy}}$ (Williams et al., 1996; Sperry et al., 2002a; Pieruschka et al., 2010) capture the priority of avoiding damage-inducing negative pressure, but fail to account for anisohydric
behavior where $P_{\text{canopy}}$ drops during water deficits. The TREES model is the closest to supply–demand theory because it uses the cavitation-based supply function to set a hydraulic limit to $E$ (Mackay et al., 2015). However, it still requires an empirical model of the stomatal response to vapor pressure deficit ($D$; Oren et al., 1999).

How good is supply–demand theory? We implement the theory in a model for predicting stomatal regulation of $E$ and $P_{\text{canopy}}$, and evaluate its behavior and realism. The model is kept simple while still incorporating heterogeneous soil and xylem properties (Fig. 1a). We compare model output with observed trends and empirical functions of stomatal responses to $D$ and soil drought. Shortcuts are examined that minimize parameterization and simplify application. We test the model’s ability to explain observed variation in canopy diffusive conductance ($G_c$) for water vapor and $P_{\text{canopy}}$ in nine data sets drawn from tropical forests with pronounced dry seasons (Wolfe et al., 2016) and from semiarid piñon-juniper woodlands (McDowell et al., 2013).

**Description**

The model is written in Visual Basic for Applications in Excel (download from http://biologylabs.utah.edu/sperry/methods.html) and in C (GCC 5.3, GNU Project). It predicts steady-state solutions at a given $D$ and bulk-soil water potential ($P_{\text{soil}}$) profile. Table 1 summarizes the parameters.

**Table 1** Model input/output, default settings, and low vs high test range

<table>
<thead>
<tr>
<th>Variable</th>
<th>Default setting (low, high)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_{\text{soil}}$, bulk soil matric potential in $N$ layers per time step</td>
<td>0 MPa (0, −8 MPa)</td>
</tr>
<tr>
<td>Continuum $k_c$ (no cavitation, saturated soil)</td>
<td>10 kg h$^{-1}$ MPa$^{-1}$ m$^{-2}$ (3, 42)</td>
</tr>
<tr>
<td>Average % resistance in rhizosphere (from $P = 0$ to $P_{\text{crit}}$)</td>
<td>5% (5, 50)</td>
</tr>
<tr>
<td>Weibull function $b$ and $c$ for root, stem, leaf (Eqn 1)$^1$</td>
<td>$b = 2$, $c = 3$, not segmented ($b = 1$, $c = 3$ sigmoid; segmented) ($b = 1.27$, $c = 1$ exponential)</td>
</tr>
<tr>
<td>Van Genuchten function $a$ and $n'$ (Eqn 2)</td>
<td>$a = 602$ MPa$^{-1}$, $n = 1.48$ (sandy clay loam)</td>
</tr>
<tr>
<td>Reversibility of cavitation (yes/no)</td>
<td>no (no, yes)</td>
</tr>
<tr>
<td>Prior drought $P_{\text{soil}}$ (irreversible cavitation only)</td>
<td>0 MPa (−2)</td>
</tr>
<tr>
<td>$G_{\text{max}}$, maximum canopy diffusive conductance to H$_2$O</td>
<td>2130 kg h$^{-1}$ m$^{-2}$ (512, 3200)</td>
</tr>
<tr>
<td>% resistance of root, stem, leaf at continuum $k_{\text{max}}$</td>
<td>50, 25, 25% (not tested)</td>
</tr>
<tr>
<td>Root depth coefficient, $\beta$</td>
<td>0.92 (not tested)</td>
</tr>
<tr>
<td>Root radial spread per maximum depth</td>
<td>1 (not tested)</td>
</tr>
<tr>
<td>Number of root and soil layers, $N$</td>
<td>1 (1, 5)</td>
</tr>
<tr>
<td>Output (per time step)</td>
<td>$\text{−}MPa$</td>
</tr>
<tr>
<td>Predawn and current $P$ canopy (xylem pressure)</td>
<td>$\text{−}MPa$</td>
</tr>
<tr>
<td>$E_c$, canopy transpiration rate</td>
<td>kg h$^{-1}$ m$^{-2}$</td>
</tr>
<tr>
<td>$G_c$, canopy diffusive conductance</td>
<td>kg h$^{-1}$ m$^{-2}$</td>
</tr>
<tr>
<td>$E_{\text{crit}}$, physical maximum transpiration rate</td>
<td>kg h$^{-1}$ m$^{-2}$</td>
</tr>
<tr>
<td>$P_{\text{crit}}$, physical minimum canopy xylem pressure</td>
<td>$\text{−}MPa$</td>
</tr>
<tr>
<td>Hydraulic conductance of root, stem, leaf</td>
<td>kg h$^{-1}$ MPa$^{-1}$ m$^{-2}$</td>
</tr>
<tr>
<td>Root water uptake from each of $N$ layers</td>
<td>kg h$^{-1}$ m$^{-2}$</td>
</tr>
</tbody>
</table>

$^1$Not segmented, identical root–stem–leaf curves; segmented, roots and/or leaves more vulnerable. Sigmoid curves retained the same $c$ parameter (Eqn 1); exponential curves had $b$ and $c$ parameters creating a nonthreshold drop from $k_{\text{max}}$. 

**Representation of the soil–plant continuum**

The continuum divides leaf, stem, root, and rhizosphere components in series (Fig. 1a). The rhizosphere is the soil around each root through which water moves down a pressure gradient from a constant-pressure water source in ‘bulk’ soil. The root and rhizosphere can be divided into up to $N$ parallel components draining $N$ horizontal soil layers (Fig. 1a).

**Fig. 2** Theoretical modes of transpiration ($E$) regulation (solid curves) relative to no regulation (gray dashed diagonal). When air is humid, unregulated transpiration $E$, representing maximum stomatal opening is low, there is little threat of cavitation, and hence there is little stomatal closure, resulting in minimal regulation of $E$ ($E = E'$, near the dashed no-regulation diagonal). As air becomes drier, $E'$ increases along with the threat of cavitation, triggering greater stomatal closure that deflects the regulation diagonal. When air is humid, $E'$ increases along with the threat of cavitation, triggering greater stomatal closure that deflects the solid curve from the dashed diagonal. Medium regulation slows the rise in $E$ relative to $E'$, followed in the driest air by maximum regulation, which keeps $E$ constant and below the hydraulic limit at $E_{\text{crit}}$ (vertical arrows from $E_{\text{crit}}$ symbols). Drier soil reduces $E_{\text{crit}}$ (compare gray (wet) and dry (black) curves), intensifying the threat of cavitation, and intensifying stomatal closure in response to drier air (gray vs black solid curves).
Each continuum component has a vulnerability curve that starts at a maximum hydraulic conductance ($k_{\text{max}}$ flow rate per pressure drop) and declines as water pressure ($P$) becomes more negative (Fig. 1b). Xylem components (leaf, stem, root) were assigned a two-parameter Weibull function:

$$k = k_{\text{max}} e^{-(P/k')^n},$$  \hspace{1cm} \text{Eqn 1}$$

where $k$ is the hydraulic conductance of the component and $P$ is the negative sap pressure in the xylem of the component (absolute value for convenience). Parameter $b$ ($P$ at $k/k_{\text{max}} = 0.37$) shifts the curve along the pressure axis, parameter $c$ controls shape (‘exponential’ shape with no threshold has $c \leq 1$, sigmoidal threshold has $c > 1$). In ‘nonsegmented’ mode, xylem components have the same curve vs ‘segmented’ mode where curves differ. The rhizosphere was assigned a van Genuchten function (van Genuchten, 1980):

$$k = k_{\text{max}} e^{[(n-1)/2a] \left[1 - \left(1 - \frac{P}{E} \right)^{(n-1)/a} - 1 \right]^2},$$  \hspace{1cm} \text{Eqn 2a}$$

$$v = \left[\left(\frac{xP_{\text{soil}}}{E} + 1\right)\right]^{-1},$$  \hspace{1cm} \text{Eqn 2b}$$

where $n$ and $a$ are tissue-specific parameters (Leij et al., 1996), and $P_{\text{soil}}$ is the absolute value of the soil water potential (assuming negligible osmotic potential). Eqn 2 is termed a ‘rhizosphere vulnerability curve’ by analogy with the xylem. Neither Eqn 1 nor 2 reaches mathematical zero, but we assumed $k < 0.05%$ of continuum $k_{\text{max}}$ was physiological zero. Sap viscosity was assumed constant.

The vascular supply function

The steady-state flow rate through each component, $E_i$, is related to the flow-induced pressure drop across that component (downstream pressure ($P_{\text{down}}$) – upstream pressure ($P_{\text{up}}$)) by the integral transform of the component’s vulnerability curve ($k(P)$ from Eqs 1 and 2):

$$E_i = P_{\text{up}} \int_{P_{\text{down}}}^{P_{\text{up}}} k(P) \, dP.$$  \hspace{1cm} \text{Eqn 3}$$

The integral transform assumes infinite discretization of the flow path, equivalent to infinitely short conduits. This is a reasonable approximation for many plants (Comstock & Sperry, 2000).

Eqn 3 is used to compute the supply function for the continuum (Fig. 1c). When there is one soil layer, the rhizosphere, root, stem, and leaf are in series. The $E_i$ is identical for each component and equal to canopy $E$. The $P_{\text{soil}}$ is known. Thus, from any $E = E_i$, the sequential pressure drops across each component are obtained from its individual integral transform (Eqn 3; excluding the gravitational drop). By solving $P_{\text{canopy}}$ in this way as $E$ is increased from zero, the $E(P_{\text{canopy}})$ supply function is calculated.

When the root and rhizosphere components are partitioned into $N$ parallel paths draining $N$ soil layers of known $P_{\text{soil}}$ there are $N+1$ unknown pressures: the $N$ root surface pressures ($\text{Rhizosphere } P_{\text{down}} = \text{root } P_{\text{up}}$) and the root crown pressure at the downstream junction for all root components (root $P_{\text{down}}$). The $N+1$ unknown pressures were solved from the following $N+1$ equations for steady-state flow:

$$E_i(\text{rhizosphere}) - E_i(\text{root}) = 0$$  \hspace{1cm} \text{Eqn 4a}$$

$$\sum E_i(\text{root}) - E = 0,$$  \hspace{1cm} \text{Eqn 4b}$$

where $E_i$ values were obtained from Eqn 3, and $E$ was specified. Eqs 4(a) ($N$ equations for $N$ layers) and 4(b) ($E_i$ sum over $N$ layers) were solved using multidimensional Newton Raphson (Press et al., 1989). Stem and leaf pressures were then obtained from Eqn 3 and the supply function generated by incrementing $E$ from zero.

The stomatal demand function

The demand function calculates $E$ and $G$ (canopy diffusive conductance to water vapor) from the atmospheric $D$ (mole fraction), $G_{\text{max}}$ (representing maximally open stomata and prevailing boundary layer conditions), and the supply function. The demand function derived in Sperry & Love (2015) (illustrated in their Fig. 2) has five steps. (1) The unregulated $E' = DG_{\text{max}}$ is located on the supply function. (2) The loss of canopy hydraulic conductance that would be caused by $E'$ was determined from the decline in the derivative of the supply function from its maximum at $P_{\text{canopy}} = P_{\text{soil}} (dE/dP_{\text{max}})$ to its value at $E' (dE'/dP_{\text{canopy}})$. The $(dE'/dP_{\text{canopy}})/(dE/dP_{\text{max}})$ fraction falls from 1 at no conductance loss to 0 for total loss at $E_{\text{crit}}$; its value represents the loss of canopy transport capacity caused by doing nothing and leaving the stomata open. (3) The unregulated soil to canopy pressure drop, $\Delta P'$, is reduced by the $(dE'/dP_{\text{canopy}})/(dE/dP_{\text{max}})$ fraction to yield the regulated pressure drop:

$$\Delta P = \Delta P' \left[ (dE'/dP_{\text{canopy}})/(dE/dP_{\text{max}}) \right].$$  \hspace{1cm} \text{Eqn 5}$$

Mathematically, $\Delta P$ rises to a maximum before decreasing back to zero as $E'$ increases to $E_{\text{crit}}$. This decline in $\Delta P$ is unrealistic (Salindra et al., 1995), so it is assumed that $\Delta P$ saturates at its maximum as $E'$ increases. Eqn 5 expresses the outcome that xylem pressure is regulated in proportion to the damage caused by taking no action. (4) The regulated $E$ corresponding to $\Delta P$ is determined from the supply function. (5) The $G$ is solved from $E/D$ to determine how much it is reduced below $G_{\text{max}}$. The model does not partition $G$ into stomatal vs boundary layer components, but $G$ is controlled by stomatal regulation. Cuticular water loss is assumed to be zero.

Reversible vs irreversible cavitation

The model runs in reversible and irreversible cavitation modes. In reversible mode, xylem hydraulic conductances track the original vulnerability curves ($k(P)$ = Eqn 1) regardless of $P$ fluctuation. In irreversible mode, the drop in xylem conductance is permanent, and the $k(P)$ vulnerability curves change from the original.
For $P = 0$ to $P_{\text{min}}$ (most negative $P$ already experienced by the conductance element), $k = k(P_{\text{min}})$. For $P$ more negative than $P_{\text{min}}$, the $k(P) = \text{Eqn 1}$. The supply function changes accordingly. Importantly, the demand function still calculates $\Delta P$ from the original uncavitated supply function; this assumes that the protective regulation of xylem pressure is immutably set by the inherent vulnerability of the continuum. The regulated $E$, however, is calculated from the current supply function as impacted by cavitation. This produces the realistic result that past cavitation does not influence $\Delta P$, but does reduce $E$ (e.g., Hacke et al., 2000; Anderegg et al., 2013, 2014). When running in irreversible cavitation mode, the model can be initialized to prior exposure to a minimum $P_{\text{soil}}$ (Table 1). Rhizosphere vulnerability curves were fully reversible in either cavitation mode.

**Maximum hydraulic conductances ($k_{\text{max}}$)**

The maximum hydraulic conductance of the continuum in the absence of any cavitation (continuum $k_{\text{max}}$) is an input parameter, as is its division into root, stem, and leaf $k_{\text{max}}$ components as required for Eqn 1. Rhizosphere $k_{\text{max}}$ (i.e. saturated soil) was large enough to be a negligible component of continuum $k_{\text{max}}$. Hydraulic conductances were usually expressed per trunk basal area. Hence the transpiration rate and canopy diffusive conductance to water vapor ($G = E/D$) were also expressed per trunk basal area.

We solved for the rhizosphere $k_{\text{max}}$ from an inputed ‘average % rhizosphere resistance.’ The % of continuum resistance in the rhizosphere was calculated from the in-series vulnerability curves of rhizosphere, root, stem, and leaf at the same $P$ (Eqns 1, 2). The % rhizosphere resistance was averaged over 0.1 MPa increments from $P = 0$ to $P_{\text{crit}}$. The rhizosphere % was negligible at $P = 0$ but can become significant with more negative $P$ because of the steep drop in the rhizosphere vulnerability curve (Eqn 2). The lower the % average rhizosphere resistance, the greater the area of absorbing roots per trunk basal area, and the thinner the rhizosphere. We specified rhizosphere resistance (via rhizosphere $k_{\text{max}}$; Eqn 2) rather than calculating it from rhizosphere geometry and root area (as in Sperry et al., 1998).

Root and rhizosphere components could be partitioned into $N$ paths draining horizontal soil layers. Layer depths were set so each layer included equal root biomass based on the function (Jackson et al., 1996):

$$B = 1 - \beta^d,$$

**Eqn 6**

where $B$ is the fraction of biomass above depth $d$ in cm, and $0 < \beta < 1$. Maximum root depth was set at $B = 0.995$ (99.5% root biomass). The rhizosphere $k_{\text{max}}$ for the whole root system was partitioned equally among the $N$ layers. Total root system $k_{\text{max}}$ was divided among layers in proportion to the inverse of the transport distance to each layer. Transport distance was depth to the center of layer biomass plus the radial spread of roots within each layer. The radial spread for the top layer was calculated by multiplying maximum root depth by an inputed aspect ratio of maximum radial spread divided by maximum root depth. The rooted soil volume in the top layer was calculated as a cylinder from spread and layer thickness. By assuming this volume was constant for each layer, the radial root spread in deeper soil layers was calculated.

**Comparison of measured vs modeled $P_{\text{canopy}}$ and $G$**

We tested the model against nine published data sets (Table 2; methods detailed in McDowell et al., 2013; Wolfe et al., 2016) consisting of vulnerability curves, soil type, and a time course of predawn $P_{\text{canopy}}$ and midday $P_{\text{canopy}}$, $D$, and $G$ measured on individual trees and on sunny days (summary data in Supporting Information Table S1). All data sets included major drought events. The ‘tropical tree’ data sets (Wolfe et al., 2016) consisted of seven, 2 yr time-courses, split between three species in a tropical dry forest (pronounced dry season) and four species in a tropical transitional forest (moderate dry season). One species was common between sites (Table 2). Each time course was assembled by averaging four to 10 trees per species/site. Species/site-specific vulnerability curves were only available for stems (P50 values (pressure at 50% loss of hydraulic conductance), cited in Table 2; curves in Fig. S1), so the model was not segmented. The piñon (Pinus edulis) and juniper (Juniperus monosperma) data sets (McDowell et al., 2013) consisted of 4 yr time-courses (April–October growing season) for six trees per species. Fluxes and conductances were on a sapwood area basis. Vulnerability curves were available for stems (both species) and roots (P. edulis).

The model was set to $N = 1$ soil layer with $P_{\text{soil}} = \text{measured predawn } P_{\text{canopy}}$ and it was run for each time series of predawn pressure and midday $D$ to predict midday $P_{\text{canopy}}$ and $G$. Predicting from predawn xylem pressure eliminated having to specify root system depth and aspect ratio, soil layers, and $P_{\text{soil}}$ profile.

The model was fitted to each data set via adjustment of three unknown inputs: the % rhizosphere resistance, continuum $k_{\text{max}}$, and $G_{\text{max}}$. Although the data sets included $k$ and $G$ (Table S1), they did not include conditions maximizing them (high light, very low $D$, and prolonged wet periods). No prior drought input was necessary because test runs confirmed its influence was largely compensated for by the tuning of $k_{\text{max}}$, $G_{\text{max}}$, and % rhizosphere (Methods S1). To equalize weighting across $G$ and $P_{\text{canopy}}$, each value was ‘studentized’ by subtracting the respective measurement mean and dividing by the standard deviation. The absolute error averaged across studentized $G$ and $P_{\text{canopy}}$ was minimized by adjusting $G_{\text{max}}$, $k_{\text{max}}$, and % rhizosphere with the downhill simplex algorithm, making every effort to ensure global minimums were found (Nelder & Mead, 1965; Methods S1). Although $G$ and $P_{\text{canopy}}$ were fitted simultaneously, we report individual $G$ and $P_{\text{canopy}}$ mean absolute errors and $\bar{r}^2$ values. Best fits were found for irreversible vs reversible cavitation settings. The piñon and juniper data sets were fitted at the individual tree level and subdivided into separate years to allow for off-season adjustments in the three fitting parameters (McDowell et al., 2013). Best-fit results for each tree were pooled to obtain the species fit.
Three modes of transpiration (E) regulation

The behavior of E in response to D and $P_{soil}$ was determined for default settings (Table 1). The demand function produced three modes of E regulation (Fig. 2). When D was low, there was little threat from canopy cavitation ($(dE/dP_{canopy})/(dEdP_{max}) \approx 1$), resulting in minimal regulation where regulated $E \approx$ unregulated $E$ (Fig. 2 ‘minimal’ portion of curve). As D rose and the threat of canopy cavitation increased ($(dE/dP_{canopy})/(dEdP_{max}) < 1$), medium regulation slowed the rise in E relative to E (Fig. 2 ‘medium’). At highest D, the threat of cavitation was maximized ($(dE/dP_{canopy})/(dEdP_{max})$ approached 0), and maximum regulation capped E at a physiological limit well within the physical limit of $E_{crit}$ (Fig. 2 ‘maximum’). Soil drying suppressed $E_{crit}$, intensified regulation, and caused reduction in the physiological $E$ limit (Fig. 2 compare grey vs black curves). The regulation of $E$ (Fig. 2) yielded the stomatal control of canopy diffusive conductance ($G = E/D$). At minimal regulation, $G \approx G_{max}$, and at maximum regulation $G$ fell in inverse proportion to D.

Stomatal response to D

The stomatal response to D was obtained by incrementing D while holding other inputs constant. The default response (Fig. 3a, curve 1; settings in Table 1) showed the typical reduction in G from $G_{max}$ in response to increasing D. However, the D threshold causing $G < G_{max}$ depended on model inputs as documented in a full sensitivity analysis (Figs S2, S3). Key trends are evident from changing inputs one at a time from the default to high vs low ends of the test range indicated in Table 1. Inputs that increased the D threshold for stomatal closure were: increased continuum $k_{max}$ (Fig. 3a, curve 2), a more resistant sigmoid vulnerability curve (curve 3; $b$ from 2 to 4; Table 1), and lower $G_{max}$ (curve 10). Inputs that accelerated stomatal closure were: lower $k_{max}$ (curve 4), a weaker sigmoid vulnerability curve (curve 5; $b$ from 2 to 1), an exponential vulnerability curve (curve 6, $b = 1.27$, $c = 1$), drier soil (curve 7; $P_{soil} = -2$ MPa), exposure to prior drought without xylem refilling (curve 8; $P_{soil} = 0$ after exposure to $P_{soil} = -2$ MPa), and increasing $G_{max}$ (curve 9). Increasing the average % rhizosphere resistance (from 5% to 50%; Table 1) had no effect because rhizosphere resistance at default $P_{soil} = 0$ is always 0%.

The $G$ by D response curves in Fig. 3(a) compared well with empirical functions used to model the D response. In these comparisons, the D range was restricted to 1–4 kPa (incremented by 0.3 kPa) to exclude extremes not well represented by observation. Within this range, $G$ exactly followed the equation, $G = g_1/D$ ($g_1$ = fitted coefficient; Lloyd, 1991), as expected during maximum regulation when $G \ll G_{max}$ (curves 1 and 3–9; $r^2 = 1.0$). This inverse model broke down for minimal-to-medium regulation when $G$ was near $G_{max}$ (curves 2 and 10), even when adding the additional fitting
coefficient \( g_o: G = g_o + g_i/D \) \((r^2 = 0.79)\). Maximum regulation was also closely approximated \((r^2 0.98–0.99)\) by the inverse square root function: \(G = g_o + g_i/D^{1/2}\) (Lloyd, 1991), and the hyperbolic function: \(G = g_o + g_i/(1 + D)\) (Leuning, 1995).

These functions gave improved fits for minimal-to-medium regulation \((r^2 0.86–0.88)\). The final empirical model tested was the equation \(G = G_{ref} - m \ln(D)\), where \(G_{ref}\) is \(G\) at \(D = 1\) kPa (Oren et al., 1999). This was the least tight of the functions for maximum regulation \((r^2 = 0.93)\), but comparable to the best for minimal-to-medium regulation \((r^2 = 0.86)\).

Greater \(G_{ref}\) has been observed to covary tightly with increasing \(m\) with a highly conserved slope of 0.56–0.6. This slope is predicted for maximum regulation, where \(P_{canopy}\) is being homeostatically regulated (Oren et al., 1999). Shallower slopes coincide with less strict regulation that allows \(E\) to increase (and \(P_{canopy}\) to become more negative). Consistent with observation, the slope of \(G_{ref}\) vs \(m\) was 0.59 for maximum regulation (Fig. 3b, curves 1, 3–9), and the response fell below the 0.59 slope for minimal-to-medium regulation (Fig. 3b, curves 2, 10).

**Stomatal response to soil moisture deficit (\(P_{soil}\))**

The stomatal response to \(P_{soil}\) was obtained by holding \(D\) constant and decrementing \(P_{soil}\) from 0 to \(-8\) MPa. Closure in drier soil occurred with varying sensitivity relative to the default response (Fig. 4, curve 1). Trends from the sensitivity analysis (Fig. 5) are illustrated by altering settings one at a time exactly as for the \(D\) response (numbered curves in Figs 3 and 4 have identical settings). Inputs that increased \(G\) relative to the default curve were: greater continuum \(k_{max}\) (Fig. 4 curve 2), a more resistant sigmoid vulnerability curve (curve 3), and a lower \(D\) (curve 12; 0.5 kPa vs default of 1.0 kPa). Increasing \(G_{max}\) had no effect because \(G\) was already below \(G_{max}\) in the default. Inputs that decreased \(G\) were: reduced \(k_{max}\) (curve 4), a weaker sigmoid vulnerability curve (curve 5), the exponential vulnerability curve (curve 6), previous exposure to drought (curve 8), greater \(D\) (curve 13; 4 kPa), and lower \(G_{max}\) (curve 10). In drying soil, an increase in the average rhizosphere resistance also caused more closure (curve 11).

**Regulation of xylem pressure (\(P_{canopy}\)) in response to drought**

Plotting midday \(P_{canopy}\) vs predawn \(P_{canopy} (= P_{soil})\) from the \(P_{soil}\) responses of Fig. 4 revealed diverse stomatal regulation of xylem pressure in response to drought (Fig. 5). The \(G_{max}\), \(k_{max}\), and \(D\) settings had no effect on \(\Delta P\) once \(E\) was capped by maximum regulation. Hence, low \(G_{max}\) (or, alternatively, high \(k_{max}\)) and low \(D\) only limited \(E\) and \(\Delta P\) in wetter soil (Fig. 5, curves 12 and 10).

Vulnerability curves largely dictated \(P_{canopy}\) regulation. A higher % rhizosphere resistance (50%) sharply limited \(\Delta P\) in medium dry soil (Fig. 5, curve 11). A more vulnerable sigmoidal xylem curve reduced the \(\Delta P\) and drove it to zero at less negative \(P_{soil}\) (curve 5). Conversely, a more resistant sigmoidal curve was
associated with a greater $\Delta P$, which declined to zero at more negative $P_{\text{soil}}$ (curve 3). The exponential vulnerability curve produced a near-constant $\Delta P$ (curve 6), because its flat tail produced relatively little cavitation and a near-constant $dE/dP$ derivative. The usually curved theoretical midday vs predawn $P_{\text{canopy}}$ relationship was approximated by a linear regression to compare simulated slope and intercept with observations (Martinez-Vilalta et al., 2014; Fig. 6). Regressions excluded extreme tails of droughted plants with > 75% loss of plant hydraulic conductance (assumed rare in observations). Default inputs were used except for the rhizosphere resistance which declined to zero at more negative $P_{\text{soil}}$ as $G_{\text{max}}$ increased from 0.2 (most isohydric) to 1.2 (most anisohydric) as the shape parameter ($c$, dashed horizontal curves) of the Weibull function vulnerability curve changes from extreme sigmoidal ($c=20$) to extreme exponential ($c=0.7$). The intercept (the soil–canopy pressure drop for wet soil) increases as the Weibull $b$ parameter (solid vertical curves) increases up to the point where $G_{\text{max}}$ limits the pressure drop. Without a $G_{\text{max}}$ limit, the intercept would continue to increase (dotted line; Supporting Information Fig. S5). Gray symbols are data from Martinez-Vilalta et al. (2014).

Responses to soil heterogeneity

Responses to soil heterogeneity were determined by dividing the root zone into $N$ soil layers of differing $P_{\text{soil}}$. A $P_{\text{soil}}$ profile (Fig. 7, gray symbols and line) resulted in a flow profile (Fig. 7, gray symbols and line), which predicted hydraulic redistribution from wet to dry layers when $E$ was low. For ‘predawn’ conditions where $E=0$, the point on the flow profile where water was neither taken up nor released (Fig. 7, zero flow line) coincided with the predawn xylem pressure on the $P_{\text{soil}}$ profile (Fig. 7, predawn arrow). This was true regardless of the shape of the $P_{\text{soil}}$ profile.

The model’s steady-state outputs were dependent solely on the predawn xylem pressure, regardless of the underlying heterogeneity of $P_{\text{soil}}$. Numerically identical results were obtained whether there were $N>1$ layers vs $N=1$, as long as the predawn xylem pressure was identical (data not shown). This important result simplified model testing because predawn xylem pressure could substitute for usually incomplete measurements of soil moisture and root profiles.

Influence of vulnerability segmentation

Vulnerability segmentation refers to differences in vulnerability curves along the soil–plant continuum (Tyree et al., 1993). The simulations shown so far (Figs 2–7) assumed no xylem segmentation. But the rhizosphere curve (Eqn 2) is inevitably different from any xylem curve (Eqn 1). The setting for the average % of rhizosphere resistance determines whether flow is more limited by the rhizosphere or the xylem. The default of 5% corresponded to a xylem-limited continuum. This setting assumes that the plant invests sufficiently in root area (and hence rhizosphere $k_{\text{max}}$) to realize the xylem’s potential for water extraction. The average rhizosphere resistance had to be increased from 1% to...
between 10% (clay, fine-textured extreme) and 20% (sandy loam, coarse-textured extreme) before the reduction in $E$ (averaged over the $P_{\text{soil}}$ range permitting $E > 0$) exceeded 5% because of an increasing soil limitation.

A single xylem vulnerability curve required only one version of Eqn 1 and eliminated the need to parse continuum $k_{\text{max}}$ into root, stem, and leaf components. However, the typical segmentation is for roots and leaves to be more vulnerable than stems (Sperry et al., 2002b; Hao et al., 2008). If the more available stem vulnerability curve was applied throughout as a substitute for typical segmentation, $E$ was overpredicted (Fig. 8a). However, as long as root and/or leaf P50 was within 0.85 × stem P50 (assuming sigmoidal curves that vary $b$ for constant $c = 3$ in Eqn 1), the overestimation was < 10% (comparing mean $E$ values across the full $E > 0$ range; Fig. 8a, shaded area).

The best no-segmentation substitute curve was the combined stem and leaf vulnerability curve (Fig. 8b). This curve was found by fitting a new Weibull function to the in-series leaf and stem $k$ computed from Eqn 1. By substituting the combined leaf-stem curve, the actual leaf and root P50 could drop below 0.5 × stem P50 without causing > 10% error as long as leaf and root P50 values were within c. 30% of each other (Fig. 8b, shaded area). Outside of this zone, error increased, especially if roots were much more vulnerable than leaves. If the root, stem, and leaf curves are all known, a near perfect substitute curve could be solved for by retrofitting the nonsegmented model to its previous segmented output.

### Quantitative model tests

In irreversible cavitation mode, the model tracked the large range in $G$ and $P_{\text{canopy}}$ associated with wide swings in soil moisture across the nine empirical data sets (Fig. 9; Table 2; individual time series in Figs S7–S11). The model explained 30–93% of the variation in measured $G$, and 30–94% of the variation in measured $P_{\text{canopy}}$ (Table 2). Dropping the poor fit to one tropical tree (*Bursera simaruba*, Table 2), the average $r^2$ values were $r^2 = 0.76$ (range 0.56–0.93) for $G$ and $r^2 = 0.69$ (0.30–0.94) for $P_{\text{canopy}}$. The absolute error in $P_{\text{canopy}}$ (absolute value of measured vs modeled difference) across all data sets averaged 0.29 MPa. In relative terms, the $P_{\text{canopy}}$ error averaged 15.0% of the mean measured value per data set (range: 11.4–23.3% Table 2; excluding *B. simaruba*). The % error in $P_{\text{canopy}}$ error averaged 15.0% of the mean measured value per data set (range: 11.4–23.3% Table 2; excluding *B. simaruba*). The % error in $G$ averaged 31.4% (13.2–38.5). The best fits were obtained at $G_{\text{max}}$ averaging 4.1 standard deviations above the observed mean $G$, and $k_{\text{max}}$ averaging 2.7 standard deviations above mean $k$ (Table 2), consistent with $D$ and cavitation tending to reduce measured values below their maxima. Fitting resulted in a consistently high value for % rhizosphere resistance (67% on average (range: 43–86%); Table 2).

The poor fit to *B. simaruba* (and, to a lesser extent, *P. edulis*) was associated with inability to track high-amplitude $G$ fluctuations in the absence of corresponding shifts in $P_{\text{soil}}$ or $D$ (Figs S8a,b, S11c,d). These species also exhibited midday xylem pressures that were often less negative than predawn values during dry periods (Wolfe et al., 2016). This cannot be predicted by the model with only one soil layer.

The model fit in reversible cavitation mode was essentially indistinguishable from the irreversible fit (Table S2; Fig. S12). There was no major effect on $P_{\text{canopy}}$ as expected from the model assumption that the soil to canopy pressure drop is unaltered by...
previous drought. The fit to $G$ was also practically the same: the average $r^2$ per data set was unchanged at 0.76, and the error per data set averaged 31.5% (vs 31.4%, excluding B. simaruba; refilling did not improve this fit, nor that of P. edulis). The $G_{\text{max}}$ and $k_{\text{max}}$ required to achieve the similar fit dropped in at least seven of the nine data sets, by an average of 26% ($G_{\text{max}}$) and 29% ($k_{\text{max}}$), compensating for the refilling setting. There was only minor reduction in the average % rhizosphere setting to an average of 64% from 67%.

**Discussion**

The supply–demand theory captured observed trends in stomatal regulation of $E$ and $P_{\text{canopy}}$ in response to $D$ and soil drought while also explaining differences in response sensitivity. With 13 inputs (Table 1), model implementation was relatively simple. The parameters are all traits, most which are measurable. Although vulnerability curves are essential, they are plentiful, and it is arguable that they are required if stomatal responses to drought are ever to be predicted effectively. Any continuum model with water flux that incorporates soil physics (and most do), should be incorporating the analogous physics of xylem.

Importantly, the supply–demand model predicted empirical response functions rather than being based on them. The theoretical $D$ response was approximated by empirical $D$ models, but the theory avoids having to know how empirical coefficients (e.g. $g_0$, $g_s$, $m$) shift between functional types and with drying soil. The slight decrease in $E$ at high $D$ that is seen in some data sets (Monteith, 1995), and which can also cause the slope of $m$ vs $G_{\text{sat}}$ to exceed 0.6 (Fig. 3b; Oren et al., 1999), is at variance with the theoretical saturation of $E$ (Fig. 2). However, even a slight decline in $P_{\text{soil}}$ can cause $E$ to decline independently of $D$ (Fig. 4), suggesting the difficulty of measuring a pure $D$ response (particularly in the field where high $D$ often corresponds with drier soil).

The supply–demand theory integrates the $D$ response with the soil drying response without requiring an empirical soil moisture response function (Fig. 4). Many large-scale models rely on a ‘water stress factor’ (Jarvis, 1976; Stewart, 1988; Powell et al., 2013) that reduces $G$ at a given $D$ as needed to obtain closure as soil water content drops (e.g. scaling the empirical $D$ response equation). The mathematical form of the water stress factor is even less constrained than empirical models of the $D$ response (Powell et al., 2013), which leads to a poor ability to predict the drought response and how it differs across species.

Empirical response functions for $P_{\text{canopy}}$ have also been proposed for distinguishing functional types in models. The slope of midday $P_{\text{canopy}}$ response to predawn xylem pressure (e.g., Fig. 5) can quantify the iso- (slope closer to 0) to anisohydric (slope closer to 1 or above) spectrum (Martínez-Vilalta et al., 2014). Theory predicted nearly the full empirical range of slopes
(0.2–1.4) and \( \Delta P \) intercepts (Fig. 6). For the nonsegmented, xylem-limited model (Fig. 6), exponential vulnerability curves (Weibull \( c \leq 1 \)) produced a slope of 1 (‘isohydric dynamic’; Franks et al., 2007) or above (‘extreme anisohydry’; Martínez-Vilalta et al., 2014) and sigmoidal curves (\( c \gg 1 \)) produced shallower slopes. In segmented mode, however, the impact of any particular curve shape (rhizosphere, root, stem, leaf) will be damped by the integrated influence of all curves in the network.

The supply–demand model explained most of the variation (up to 94%) in measured \( P_{\text{canopy}} \) and \( G \) in response to wide fluctuations in environmental conditions with an average mean absolute error < 26% (Figs 9, S7–S11; Table 2). The small difference between reversible vs irreversible model fit resulted from adjustment of the fitting parameters (\( G_{\text{max}} \), continuum \( k_{\text{max}} \), % rhizosphere resistance) in response to changing the reversibility setting. The data sets lacked conditions for robust estimates of \( G_{\text{max}} \) and \( k_{\text{max}} \) (low \( D \), high light, prolonged wet soil record), which would allow for a better test of the influence of reversibility. The % rhizosphere resistance is difficult to measure directly (Bristow et al., 2008b) and will probably always be a tunable parameter.

The % rhizosphere resistance required to fit the model was much higher (67% on average) than the 10–20% xylem vs soil threshold, suggesting a strong soil limitation. However, it is likely that high soil vulnerability was substituting in part for missing leaf and root vulnerability curves. Leaves and roots are often more sensitive to cavitation than stems, and can greatly influence the model (Fig. 8) in the same general way as an increased soil limitation. Model experiments on our data sets (Notes S1) demonstrated that segmented output (root and leaf P50 half that of the stem) at a 5% rhizosphere setting could be fitted with unsegmented output (stem only) by tuning \( G_{\text{max}} \), \( k_{\text{max}} \) and % rhizosphere. Rhizosphere % increased to an average of 76% and error dropped to an average of 25% (from 144%). \( G_{\text{max}} \) and \( k_{\text{max}} \) changed comparatively little. The % rhizosphere and error values in these simulated fits were typical of our best actual fits (Table 2), indicating that elevated rhizosphere resistance could indeed be compensating for missing segmentation. More rigorous theory testing will require data sets collected for the purpose.

Vulnerability segmentation of xylem is a practical hurdle to implementing the theory. Although stem vulnerability curves are common, root and leaf curves are much less so. If more segmentation data were collected, patterns should emerge that would simplify parameterization. Our sensitivity analysis suggests that if the root/stem and leaf/stem P50 ratios are between 0.85 and 1.0, the root and leaf curves can be ignored (Fig. 8a). Unfortunately, a sampling of the literature produced only c. 4% of root vs stem comparisons (24 species, Sperry et al., 2002b) and 12% of leaf vs stem comparisons (17 species, Tyree et al., 1993; Jacobson et al., 2007; Hao et al., 2008; Brodribb & Cochard, 2009; Scoffoni et al., 2011) in this category. Alternatively, if the root/stem and leaf/stem P50 ratios are similar, a combined branch plus leaf curve may be an adequate substitute (Fig. 8b). In the same literature sample, the root/stem P50 ratio ranged from 0.15 to 0.95 and the leaf/stem P50 ratio was in the range 0.36–1.2. Although these ratios were from different species, their similar range is consistent with a similar magnitude in vulnerability segmentation of roots and leaves. A combined branch plus leaf vulnerability curve can be measured in combination using the dehydration method (Kolb et al., 1996) and may be the best option if just a single curve is used. It was possible to obtain a single xylem curve that accurately represented segmentation, but this required knowing the segmentation, or else solving for a ‘hybrid’ xylem curve by fitting data. Identifying emergent patterns of vulnerability segmentation would make this single-curve approach feasible.

A broader impact of supply–demand theory is to improve inputs into models of larger-scale processes, thereby improving predictions of responses to water deficits in air and soil. The theoretical \( E \) response in tandem with a layered root system constrains hydrologic models of soil water draw-down and ecosystem water flux (Brooks et al., 2011; Chen et al., 2015). The water-limited \( G \) response can be translated into drought-limited photosynthesis and productivity by existing models (Farquhar & Caemmerer, 1982; Le Roux et al., 2001). The TRESs model is an example of how hydraulic constraints on \( G \) can be integrated with stomatal responses to light, \( \text{CO}_2 \), and photosynthetic rate (Mackay et al., 2015). The \( P_{\text{canopy}} \) response limits tissue growth, turgr, and phloem transport (Tyree & Hammel, 1972; Cosgrove, 1997; Sevanto, 2014). The cavitation response contributes to drought memory (Anderegg et al., 2013, 2015). Although all of these responses can contribute to tree mortality, the linkage is best established for the cavitation response. Cavitation-induced losses of 60% or more in tree hydraulic conduc-
tance are associated with subsequent mortality (Rice et al., 2004; Hoffmann et al., 2011; Anderegg et al., 2012; Kukowsi et al., 2013; McDowell et al., 2013; Url et al., 2013; Anderegg, 2014). A mortality threshold < 100% suggests death can occur without complete loss of a water supply. Thus, even a stomatal demand function that avoids \( E_{\text{crit}} \) can ultimately be lethal, owing to complications from low gas exchange and extreme \( P_{\text{canopy}} \).

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Author contributions

J.S.S. led theory development, wrote the VBA model, designed the research, led the analysis, and wrote the paper. Y.W. participated in theory development, wrote the C model version, and assisted in analysis. B.T.W. collected data on tropical forest species, and assisted in model analysis. D.S.M. and W.R.L.A. assisted in theory development and edited the manuscript. N.G.M. provided data on pinyon pine and juniper, and edited the manuscript. W.T.P. provided data on pinyon pine and juniper.

References


Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Vulnerability curves for modeled species.

Fig. S2 Vulnerability curves for sensitivity analysis.

Fig. S3 Sensitivity of canopy diffusive conductance (G) to vapor pressure deficit (D).

Fig. S4 Sensitivity of canopy diffusive conductance (G) to soil water potential (Psoil).

Fig. S5 Fig. 6 from the text, but with unlimited maximum canopy diffusive conductance (Gmax).

Fig. S6 Effect of the % rhizosphere setting on Fig. S5.

Figs S7–S11 Time sequence of modeled vs measured G and Pcanopy for each modeled species.

Fig. S12 Model vs measured G and Pcanopy for reversible cavitation mode.

Table S1 Data set parameters

Table S2 Model fit statistics for reversible cavitation mode

Methods S1 Model fitting.

Notes S1 Model experiments on % rhizosphere compensation.

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