Stomatal regulation prevents plants from critical water potentials during drought: Result of a model linking soil–plant hydraulics to abscisic acid dynamics

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Abstract
Understanding stomatal regulation during drought is essential to correctly predict vegetation-atmosphere fluxes. Stomatal optimization models posit that stomata maximize the carbon gain relative to a penalty caused by water loss, such as xylem cavitation. However, a mechanism that allows the stomata to behave optimally is unknown. Here, we introduce a model of stomatal regulation that results in similar stomatal behaviour without presupposing an optimality principle. By contrast, the proposed model explains stomatal closure based on a well-known component of stomatal regulation: abscisic acid (ABA). The ABA level depends on its production rate, which is assumed to increase with declining leaf water potential, and on its degradation rate, which is assumed to increase with assimilation rate. Our model predicts that stomata open until the ratio of leaf water potential to assimilation rate, proportional to ABA level, is at a minimum. As a prerequisite, the model simulates soil–plant hydraulics and leaf photosynthesis under varying environmental conditions. The model predicts that in wet soils and at low vapour pressure deficit (VPD), when there is no water limitation, stomatal closure is controlled by the relationship between photosynthesis and stomatal conductance. In dry soils or at high VPD, when the soil hydraulic conductivity limits the water supply, stomatal closure is triggered by the sharp decline in leaf water potential as transpiration rate increases. Being adaptive to changing soil and atmospheric conditions, the proposed model can explain how plants are enabled to avoid critical water potentials during drought for varying soil properties and atmospheric conditions.

KEYWORDS
abscisic acid (ABA), drought, root water uptake, soil–plant hydraulics, stomatal regulation

1 | INTRODUCTION

Stomata regulate gas exchange between plants and the atmosphere allowing plants to take up CO₂ while controlling water loss. During drought, uncertainties in stomatal behaviour challenge the predictions of vegetation-atmosphere fluxes (Trugman et al., 2018). It includes uncertainties related to future terrestrial carbon cycling and underscores the need to better understand stomatal behaviour during drought.

Stomata adjust to drought conditions by reducing plant water loss. This is a response to declining plant water status and has been
classified into ‘hydropassive’ and ‘hydroactive’ mechanisms (Buckley, 2019). The ‘hydropassive’ mechanism describes stomatal movement based on passive water flow into and out of the guard cells in direct response to changes in leaf water potential (Buckley et al., 2003). By contrast, abscisic acid (ABA) mediates ‘hydroactively’ the closing of stomata by causing a change in the osmotic potential of guard cells (e.g., Buckley, 2019; Kuromori et al., 2018; Tardieu & Davies, 1993; Wilkinson & Davies, 2002). Modelling approaches at the cellular level (Li et al., 2006; Buckley & Mott, 2013) are not easily applicable for predicting stomatal responses under varying atmospheric and soil conditions (Venturas et al., 2017).

Thus, other modelling approaches are used for this purpose. On the one hand, many vegetation models utilize empirical descriptions (Medlyn et al., 2011) that correlate stomatal conductance to photosynthesis (Ball et al., 1987; Leuning, 1995). However, the predictive value of these empirical models is doubtful under changing atmospheric and soil conditions (Trugman et al., 2018), and the performance seems poor during drought as indicated by an overestimation of leaf gas exchange (Anderegg et al., 2017).

On the other hand, stomatal optimization theory offers an approach to predict stomatal conductance and leaf gas exchange under any environmental condition (Wang et al., 2020). Such optimization models assume that stomata optimize the trade-off between photosynthetic carbon gain and transpirational water loss (Cowan & Farquhar, 1977; Wang et al., 2020). Currently, there is a tendency to quantify the water penalty by the risk of xylem cavitation (Sperry et al., 2017; Wang et al., 2020; Wolf et al., 2016). It suggests that a reduction in xylem conductance due to cavitation triggers stomatal closure and limits water flow under drought conditions. However, recent studies show that stomatal closure precedes the onset of cavitation and is not the consequence of reduced xylem conductivity (Brodribb et al., 2016, 2017; Choat et al., 2018; Hochberg et al., 2017; Martin-StPaul et al., 2017; Rodríguez-Domínguez & Brodribb, 2020). Furthermore, the outer xylem tissue dehydrates and plausibly loses its hydraulic conductivity even before xylem cavitation occurs (Albuquerque et al., 2020; Cardoso et al., 2020).

Regardless of the primary cause of loss in hydraulic conductivity, stomatal behaviour must fit to soil–plant hydraulic properties in order to prevent plants from critical water potentials (Carminati & Javau, 2020; Sperry & Love, 2015). As the hydraulic regime can change spatially (e.g., soil properties) and temporally (e.g., VPD), stomatal responses should be adaptive to changing conditions. While stomatal responses to humidity have been studied to a considerable extent (e.g., Knauer et al., 2015; Monteith, 1995; Peak & Mott, 2011), it is unclear how stomatal closure during drought changes with soil properties (Carminati & Javau, 2020). Moreover, it is an open question which regulating principle allows the stomata to prevent an excessive (non-linear) decline in leaf water potential during drought.

Here, we introduce a model of stomatal regulation that aims to reproduce adaptive and optimal-like stomatal behaviour without presupposing an optimality principle. It explains stomatal closure based on a well-known mechanism for stomatal regulation, which is ABA. The model is based on calculations of soil–plant hydraulics and leaf photosynthesis under varying environmental conditions. It requires simulations of leaf water potentials based on transpiration rate, soil water potential and variable hydraulic conductances of key elements of the system, namely, rhizosphere, roots and xylem (Carminati & Javau, 2020). The model predicts stomatal conductance for variable VPD and soil hydraulic properties so that plants are prevented from excessive drops in water potential during drought. Finally, we discuss where model verification is primarily needed.

2 | THEORETICAL BACKGROUND AND MODELLING METHODOLOGY

The following paragraph describes the governing equations of water flow in soil and plants. The aim is to calculate leaf water potentials which lay the foundation for the stomatal regulation model presented in the subsequent paragraph. All mathematical symbols and abbreviations used in this study are listed in Table 1.

2.1 | Soil–plant hydraulic modelling

Water flow in soil and plants is driven by a gradient in water potential $\Delta \Psi$ (MPa), which depends on the transpiration rate $E$ (cm$^3$ s$^{-1}$) and a series of hydraulic conductances along the soil–plant–atmosphere continuum. The soil–plant hydraulic model used in this study stems from Carminati and Javau (2020) and is structured in three compartments: the soil, the root and the plant xylem.

In soils, water flow in the unsaturated zone is based on Richardson–Richards equation (Richards, 1931; Raats & Knight, 2018) which in radial coordinates writes to

$$\frac{\partial \theta}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left( r \cdot k(h) \frac{\partial h}{\partial r} \right),$$  \tag{1}

where $\theta$ (cm$^3$ cm$^{-3}$) is the volumetric water content, $t$ (s) is the time, $r$ (cm) is the radius, $k(h)$ (cm$^3$ s$^{-1}$) is the unsaturated soil hydraulic conductivity and $h$ (cm) is the matric head that is equal to the soil matric potential $\Psi_m$ (hPa) divided by gravity $g$ (m s$^{-2}$) and the density of water $\rho$ (kg m$^{-3}$) $h = \Psi_m / g \rho$. For radial flows to the root surface, gravity is neglected. This partial differential equation is solved analytically under the ‘steady-rate assumption’ (de Willigen & van Noordwijk, 1987; Van Lier et al., 2006; Schröder et al., 2008), that is,

$$\frac{\partial \theta}{\partial t} = a,$$  \tag{2}

where $a$ (s$^{-1}$) is the constant soil water depletion rate. Using the definition of matric flux potential $\Phi$ (cm$^2$ s$^{-1}$),

$$\Phi_t = \int_{-\infty}^{h} k(h) \, dh,$$  \tag{3}
| Term       | Definition                                      | Unit                        |
|------------|------------------------------------------------|-----------------------------|
| $a$        | Constant soil water depletion rate             | s$^{-1}$                    |
| $A$        | Assimilation rate                              | $\mu$mol m$^{-2}$s$^{-1}$   |
| $A_{\text{max}}$ | Maximum assimilation rate                      | $\mu$mol m$^{-2}$s$^{-1}$   |
| ABA        | Abscisic acid                                  | —                           |
| $[\text{ABA}]$ | Leaf ABA level near the guard cells         |                             |
| $C_1$, $C_2$ | Constants of integration                      | cm$^2$s$^{-1}$              |
| $E$        | Transpiration flow                             | cm$^3$s$^{-1}$              |
| $E_{\text{leaf}}$ | Transpirational flux density per unit leaf area | mmol m$^{-2}$s$^{-1}$       |
| $\epsilon_p$ | $\propto$ minimum production rate of ABA     | MPa                         |
| $\epsilon_A$ | $\propto$ minimum degradation rate of ABA    | $\mu$mol m$^{-2}$s$^{-1}$   |
| $g$        | Gravity                                        | m s$^{-2}$                  |
| $g_s$      | Stomatal conductance                           | mmol m$^{-2}$s$^{-1}$       |
| $g_{\text{max}}$ | Maximum stomatal conductance                  | mmol m$^{-2}$s$^{-1}$       |
| $h$, $h_b$ | Bulk soil matric head                         | cm                          |
| $h_*$      | Limit of Brooks–Corey parameterization (soil)  | cm                          |
| $\kappa$  | Constant of ABA sink term                      | —                           |
| $k(h)$    | Unsaturated soil hydraulic conductivity        | cm s$^{-1}$                 |
| $k_{\text{sat}}$ | Saturated soil hydraulic conductivity         | cm s$^{-1}$                 |
| $K_M$     | Michaelis–Menten constant                      | mmol m$^{-2}$s$^{-1}$       |
| $K_p$     | Plant hydraulic conductance                    | cm$^3$s$^{-1}$MPa$^{-1}$    |
| $K_r$     | Root hydraulic conductance                     | cm$^3$s$^{-1}$MPa$^{-1}$    |
| $K_s$     | Rhizosphere hydraulic conductance              | cm$^3$s$^{-1}$MPa$^{-1}$    |
| $K_{x_{\text{max}}}$ | Maximum xylem hydraulic conductance       | cm$^3$s$^{-1}$MPa$^{-1}$    |
| $l$       | Effective root length (active in water uptake) | cm                          |
| $L A$     | Leaf area                                      | cm$^2$                      |
| $M_{\text{H}_2\text{O}}$ | Molar weight of water                          | kg mol$^{-1}$               |
| $p_{\text{atm}}$ | Atmospheric pressure                           | kPa                         |
| $\Phi$    | Matric flux potential                          | cm$^3$s$^{-1}$              |
| $\Psi_m$, $\Psi_{\text{leaf}}$ | Leaf water potential                      | MPa                         |
| $\Psi_m$  | Soil matric potential                          | hPa                         |
| $\Psi_0$  | Water potential at the root surface            | MPa                         |
| $\Psi_r$  | Water potential within the root xylem         | MPa                         |
| $\Psi_{\text{s}}, \Psi_{\text{soil}}$ | Bulk soil water potential                   | MPa                         |
| $\Psi_{*, x}$ | Limit of Brooks–Corey parameterization       | MPa                         |
| $q$       | Buckingham–Darcy flux                          | cm s$^{-1}$                 |
| $q_0$     | Water flux at the root surface                 | cm s$^{-1}$                 |
| $r$       | Radius                                         | cm                          |
| $r_0$     | Root radius                                    | cm                          |
| $r_b$     | Rhizosphere radius                             | cm                          |
| $\rho$    | Density of water                               | kg m$^{-3}$                 |
TABLE 1 (Continued)

| Term         | Definition                  | Unit   |
|--------------|-----------------------------|--------|
| SOL          | Stress onset limit          |        |
| VPD          | Vapour pressure deficit     | kPa    |
| \( V_s \)    | Rhizosphere volume          | cm³    |
| \( t \)      | Time                        | s      |
| \( \tau \)   | Exponent of Brooks–Corey parameterization (soil) |        |
| \( \tau_x \)| Exponent of Brooks–Corey parameterization (xylem) |        |
| \( \theta \)| Volumetric soil water content | cm³ cm⁻³ |

with \( k(h) \) (cm s⁻¹) as the unsaturated soil hydraulic conductivity, the common solution of Equation (1) is given by

\[
\frac{\partial \Phi}{\partial t} + \frac{ar}{2} + \frac{C_1}{r} = -q. \tag{4}
\]

and

\[
\Phi(r) = \frac{ar^2}{4} + C_1 \ln(r) + C_2, \tag{5}
\]

where \( q \) (cm s⁻¹) is the Buckingham–Darcy flux (Sposito, 1978):

\[
q = -k(h) \frac{\partial h}{\partial t}. \tag{6}
\]

The parameters \( C_1 \) and \( C_2 \) are obtained via the following boundary conditions:

\[
\frac{\partial \Phi}{\partial t} \big|_{r=r_0} = -q_0 = -\frac{E}{2\pi L r_0}, \tag{7}
\]

\[
\Phi(r) = \Phi(r_0) = \frac{ar_0^2}{4} + C_1 \ln(r_0) + C_2, \tag{8}
\]

where \( r_0 \) (cm) is the root radius and \( r_b \) (cm) is the radius of the cylindrical soil volume \( V_s \) (cm³) around the ‘single root’ (cf. Gardner, 1960). \( L \) (cm) is the effective root length active in water uptake. Given these boundary conditions and the constant depletion rate,

\[
\frac{\partial \theta}{\partial t} = \frac{E}{V_s} \frac{E}{aL(r_b^2 - r_0^2)}, \tag{9}
\]

results in

\[
C_1 = -\frac{E}{2\pi L} \left( \frac{r_b^2}{r_b^2 - r_0^2} \right), \tag{10}
\]

and

\[
C_2 = \Phi(r_b) - \frac{E}{2\pi L} \left( \frac{r_b^2}{r_b^2 - r_0^2} \ln(r_b) \right), \tag{11}
\]

The matric flux potential at the root surface is then

\[
\Phi(r_0) = \Phi(r_b) - \frac{E}{2\pi L} \left( \frac{1}{2} \frac{r_b^2 \ln \left( \frac{h}{h_s} \right)}{r_b^2 - r_0^2} \right). \tag{12}
\]

By parameterizing the unsaturated soil hydraulic conductivity in Equation (3) according to Brooks and Corey (1964), the matric flux potential becomes

\[
\Phi = \int_{-\infty}^{h} k_{sat} \left( \frac{h}{h_s} \right)^{-\tau} dh = k_{sat} \left[ \frac{h_s}{1-\tau} \right]^{1-\tau} h, \quad h \leq h_s, \quad \tau > 1. \tag{13}
\]

\( k_{sat} \) (cm s⁻¹) is the saturated soil hydraulic conductivity, \( h_s \) (cm) the upper limit of the Brooks–Corey parameterization \( (h_s h) \), and \( \tau \) (\(-\)) determines the steepness of the conductivity decline with decreasing water potentials. Using Equation (13) for Equation (12), the water potential at the root surface \( \Psi_0 \) (MPa) is then

\[
\Psi_0 = -\frac{\Psi_b}{10^3} \frac{1}{h_b} \frac{E(1-\tau)}{2\pi L K_{sat} \left[ \frac{h_s}{1-\tau} \right]^{1-\tau}} \left( \frac{r_b^2 \ln \left( \frac{h}{h_s} \right)}{r_b^2 - r_0^2} \right)^{1-\tau}. \tag{14}
\]

To calculate the water potential along root and stem xylem, we neglect plant water storage and assume a constant hydraulic root conductance \( K_r \) (cm³ s⁻¹ MPa⁻¹). The flow from the outer root surface to inner root xylem is then

\[
E = -K_r (\Psi_0 - \Psi_r), \tag{15}
\]

and \( \Psi_r \) (MPa) is the water potential in the root xylem. The water flow along stem and root xylem is given by

\[
E = -K_r (\Psi_l - \Psi_s), \tag{16}
\]
where $\Psi_l$ (MPa) is the leaf (xylem) water potential and $K_s(\Psi_l)$ (cm$^3$ s$^{-1}$ MPa$^{-1}$) is the xylem hydraulic conductance of the plant. $K_s(\Psi_l)$ declines with decreasing water potential due to cavitation and is parameterized according to Brooks–Corey:

$$K_s(\Psi_l) = K_{s0} \left( \frac{\Psi_l}{\Psi_{s,x}} \right)^{-r_s}.$$  \hspace{1cm} (17)

$K_{s0}$ (cm$^3$ s$^{-1}$ MPa$^{-1}$) is the maximum hydraulic conductance of the xylem, $\Psi_{s,x}$ (MPa) is the water potential at which the xylem conductance starts to decrease and $r_s$ (-), describes the steepness of this decline. Finally, by using the concept of matric flux potential for the xylem, combined with the Brooks–Corey parameterization of $K_s(\Psi_l)$, the leaf water potential can be calculated as

$$\Psi_l = -\frac{E(1 - r_s)}{K_{s0}} \left[ \frac{\Psi_l}{\Psi_{s,x}} \right] + \left[ \frac{\Psi_l}{\Psi_{s,x}} \right]^{1-r_s}.$$  \hspace{1cm} (18)

The soil–plant hydraulic model results in the leaf water potential $\Psi_l$ needed to sustain a certain transpiration rate $E$ for a given soil water potential $\Psi_s$ (MPa). Together, these three variables determine the soil–plant hydraulic surface $E(\Psi_s, \Psi_l)$ of the simplified soil–plant system that exhibits the typical pattern of soil isolines in two dimensions (grey lines in the left panel of Figure 1: cf. Carminati & Javaux, 2020; Sperry & Love, 2015). The soil isolines represent at any specific soil water potential the physically possible hydraulic states of the plant. When soil and leaf water potential are equal (intercept of isolines with x axis), transpiration must cease as there is no gradient in water potential to drive the water flow. In wet soils or for small-to-medium transpiration rates, $\Psi_l$ decreases nearly linearly. As the soil dries, the isolines become non-linear. Non-linearity occurs due to xylem cavitation and decline in rhizosphere conductance ($K_{s-r}$, cm$^3$ s$^{-1}$ MPa$^{-1}$). Comparing the decrease of water potential in the soil with that occurring in the plant, that is, with the plant hydraulic conductance $K_p$ (cm$^3$ s$^{-1}$ MPa$^{-1}$)

$$K_{s-r} = -\frac{E}{\Psi_0 - \Psi_f},$$  \hspace{1cm} (19)

reveals the hydraulically limiting element of the water supply. The right panel of Figure 1 shows the decline in water potential in rhizosphere (brown) and plant (green), respectively. From this, the rhizosphere-limiting conditions can be derived (coloured in khaki). Note that in Figure 1, as in all upcoming figures, transpiration is expressed as transpirational flux density per unit leaf area $E_{leaf}$ (mmol m$^{-2}$ s$^{-1}$). The flux density is calculated as

$$E_{leaf} = \frac{10^3 \cdot \rho \cdot E}{M_{H_2O} \cdot LA},$$  \hspace{1cm} (21)

where $M_{H_2O}$ (kg mol$^{-1}$) is the molar weight of water and LA (cm$^2$) is the leaf area.

Following Carminati and Javaux (2020), we divide the soil–plant hydraulic surface in a ‘linear’ and ‘non-linear’ zone by means of the

![Figure 1](image-url)  

**Figure 1**  
Left: Exemplary simulation of leaf water potential ($\Psi_{leaf}$) for varying transpirational flux density ($E_{leaf}$) and soil water potential. The soil isolines (grey) indicate the hydraulically possible states at constant soil water potential: $E_{leaf}(\Psi_{leaf})/\Psi_s$. The default model parameters are given in Table 2. The stress onset limit (SOL, red line and enveloping colour band) divides the soil–plant hydraulic surface in a ‘linear’ and ‘non-linear’ zone. It is defined as the condition at which the slope of the soil isolines reaches 50% ± 25% of its maximum value (Equation 22). Right: Comparison of plant ($K_p$) and rhizosphere conductance ($K_{s-r}$) by means of their corresponding losses in water potential. The two different isolines depict the water potential at the root surface ($\Psi_0$, brown) and the pressure loss within the plant ($\Psi_f - \Psi_0$) added with the soil water potential ($\Psi_s$) to facilitate visual comparison (green). The conditions (transpiration rate, soil water potential) under which the rhizosphere dominates the total loss of conductance ($K_{s-r} < K_p$, i.e., $\Delta \Psi_{leaf-root} > \Delta \Psi_{root-leaf}$) are coloured in khaki.
so-called stress onset limit (SOL): It is defined as the point at which the slope of the soil isolines decreased to a fraction of its maximum value. Here, we use 50% and provide also the range between 25% and 75%:

\[
\text{stress onset limit (SOL)} \equiv 50\% \cdot \max \left( \frac{\partial E}{\partial \Psi}, \Psi_{\text{sat}} \right).
\]  

(22)

Beyond the SOL (solid red line in the left panel of Figure 1), plants are not in a favourable state, since a minor increase in transpiration leads to a disproportional decline in leaf water potential. Note that in this region, the rate at which the leaf water potential decreases can be fast, in particular in soils with steep hydraulic conductivity curves, such as sandy soils (Carminati & Javaux, 2020). Based on this argument, Carminati and Javaux (2020) proposed that stomata should promptly close around the SOL. A similar concept was proposed in Sperry and Love (2015) to constrain stomatal behaviour by soil–plant hydraulics and to avoid hydraulic failure. A stomatal regulating principle that prevents plants from getting too far into the non-linearities beyond the SOL is proposed in the following paragraph.

### 2.2 Regulation model of stomatal responses to drought

Here, we describe a model of stomatal regulation that is linked to ABA dynamics (production, degradation and transport). It results in steady-state solutions for the degree of stomatal opening which prevent plants from non-linear drops in leaf water potential for varying VPD and soil conditions. The model links to existing evidence about vent plants from non-linear drops in leaf water potential for varying steady-state solutions for the degree of stomatal opening which pre-

\[
\frac{d[ABA]}{dt} \propto \text{source} - \text{sink} \times f(\Psi_I) - f(ABA).
\]

(23)

Since little is known about the quantitative relations of ABA biosynthesis and catabolism, we use the simplest one: a linear relationship

\[
f(\Psi_I) \propto -\Psi_I + \epsilon_{\Psi},
\]

(24)

where the constant $\epsilon_{\Psi}$ (MPa) indicates a minimum production of ABA when $\Psi_I \approx 0$. For the sink term of [ABA], we consider a first-order kinetics and assume that ABA degradation is linearly related to the assimilation rate

\[
f(ABA) \propto x \cdot [ABA] = (A + \epsilon_A) \cdot [ABA],
\]

(25)

where $\epsilon_A$ (μmol m$^{-2}$ s$^{-1}$) indicates a minimum degradation of ABA when assimilation ceases ($A \approx 0$). The solution of Equation (23) under steady-state conditions is

\[
[ABA] \propto -\frac{\Psi_I + \epsilon_{\Psi}}{A + \epsilon_A}.
\]

(26)

Combining Equation (26) with the observation that $g_s$ declines with rising [ABA], that is,

\[
\frac{dg_s}{d[ABA]} \leq 0,
\]

(27)

leads to the fundamental posit of our model

\[
\frac{dg_s}{d\left(\frac{-\Psi_I + \epsilon_{\Psi}}{A + \epsilon_A}\right)} \leq 0.
\]

(28)

Equation (28) states that $g_s$ cannot increase when the ABA level, that is, the ratio of leaf water potential to assimilation rate, increases (negative feedback). This means that stomata open progressively as [ABA] declines (positive feedback) until they become restricted at the local minimum of [ABA]. That point, where $g_s$ is at the local minimum of [ABA], we define as stomatal steady-state solution

\[
\text{stomatal steady-state solution} \equiv g_{s,\text{min}[ABA]} \equiv g_s \left(\frac{-\Psi_{I,\text{min}}}{A + \epsilon_A}\right).
\]

(29)

Note that this predicts a steady-state target value for stomatal conductance which is realized through the feedback loop between $g_s$ and [ABA].

In order to determine the stomatal steady-state solutions, the assimilation rate needs to be known. For the purpose of this study,
we approximate the assimilation rate simply as a function of stomatal conductance through a Michaelis–Menten saturation curve (cf. Farquhar et al., 1980; Wang et al., 2020)

$$A(g_s) = \frac{g_s A_{\text{max}}}{g_s + K_M},$$  \hspace{1cm} (30)

where $A_{\text{max}}$ ($\mu$mol m$^{-2}$ s$^{-1}$) is the maximum assimilation rate, $K_M$ (mmol m$^{-2}$ s$^{-1}$) is the Michaelis–Menten constant which is numerically equal to the stomatal conductance at which the assimilation rate is half of $A_{\text{max}}$, and the conversion factor of 1.6 arises from the different diffusivities of H$_2$O and CO$_2$ (Tuzet et al., 2003). This dependence of assimilation rate on stomatal conductance is illustrated in Figure 2. In addition, the stomatal steady-state solutions are depicted with colours representing the range of soil water potentials, that is, from wet (blue) to dry (pink) soils. It shows how stomatal conductance and assimilation rate are greatly diminished while soils become dry.

To approximate the assimilation rate using Equation 30, stomatal conductance is needed first. Two assumptions are made to derive stomatal conductance from transpirational flux density: (a) negligible aerodynamic resistance in the thin layer of air around the leaves and (b) negligible cuticular transpiration. Then, $g_s$ can be computed from $E_{\text{leaf}}$ for a given atmospheric pressure ($p_{\text{atm}}$, kPa) and VPD (kPa):

$$g_s = \frac{E_{\text{leaf}}}{p_{\text{atm}}} \frac{\Psi_{\text{atm}}}{\text{VPD}}.$$  \hspace{1cm} (31)

Finally, with $g_s$ and $A$ obtained by combining soil–plant hydraulic and stomatal modelling, the stomatal steady-state solutions can be calculated. Figure 3 illustrates the resulting relationship of $g_s$ and [ABA] with the stomatal steady-state solutions shown in blue. Here, it is best comprehended how the dynamic interplay between $g_s$ and [ABA] determines the leaf gas exchange. Following upwards the soil isolines (grey) from the bottom-right corner (which corresponds to predawn conditions) indicates the time course of [ABA] and $g_s$ during stomatal opening. Once the stomata open, [ABA] decreases in a positive feedback loop as an increase in $g_s$ causes [ABA] to decline. At the stomatal steady-state solutions, however, an increase in $g_s$ leads to an increase in [ABA] (negative feedback) and further stomatal opening is prevented. This feedback loop between $g_s$ and ABA ultimately explains how the proposed model of stomatal regulation enables plants to avoid unfavourable hydraulic states (non-linear zone). In addition, considering the relationship between [ABA] and its driver for production ($\Psi_l$) and degradation ($A$) separately, the stomatal steady-state solutions show an expected behaviour (Figure S3): The realized ABA level (at the stomatal steady-state solutions) increases when leaf water potential and assimilation decline due to soil drying.

While many studies consider $g_s$ to be a unique function of leaf water potential (e.g., Henry et al., 2019; Klein, 2014), our stomatal model does not predict that stomata close in response to a threshold of neither $\Psi_{\text{leaf}}$ nor [ABA]. In contrast, it is the dynamic interplay of $g_s$ and [ABA] (positive/negative feedback) that determines leaf gas exchange in such a way that the hydraulic non-linearities are prevented. The interplay of $g_s$ and [ABA] itself depends on conditions.

**FIGURE 2** Illustration of photosynthetic assimilation rate ($A$) as a function of stomatal conductance ($g_s$) described by Equation (30). The stomatal steady-state solutions (open circles) for default conditions (VPD = 1 kPa, sandy loam soil) are coloured according to the range of soil water potentials, that is, from wet (blue) to dry (pink) soil conditions.

**FIGURE 3** The effect of ABA level, [ABA], on stomatal conductance ($g_s$) determines the stomatal steady-state solutions (blue) at the local minima of [ABA]. The time course of [ABA] and $g_s$ during stomatal opening can be comprehended by following the soil isolines (grey) upwards from the bottom-right corner (which corresponds to predawn conditions). Once the stomata open, the increase in $g_s$ causes [ABA] to decrease (positive feedback). However, after the stomatal steady-state solution is reached, the feedback loop turns into a negative mode, because a further increase in $g_s$ leads to an increase in [ABA]. Thus, further stomatal opening is prevented or reversed.
of water supply and demand. This allows the stomata to respond flexibly to different hydraulic circumstances, which is elucidated in this study by examining the model under specific environmental scenarios.

2.3 | Environmental sample scenarios

We study the response of stomatal closure to water deficit under different climates and soils. The default conditions are set to represent a sandy loam soil at a VPD = 1 kPa. Humid and dry air conditions are simulated with VPD of 0.3 and 3 kPa, respectively. Variable water supply conditions are modelled by considering contrasting soil textures (loamy and sandy soil). The respective soil hydraulic properties are parameterized according to Brooks–Corey with $k_{sat}$: $10^{-4}$, $10^{-3}$ and $2 \times 10^{-5}$ (cm s$^{-1}$), $r$: 2.6, 3 and 2 (–); and $h$: −25, −10 and −100 (cm), corresponding to a sandy loam, sand and loam, respectively. All other parameters of the soil–plant hydraulic (e.g., root length) and of the stomatal model remain constant in the analysis and are listed in Table 2. The different soil hydraulic conductivities are illustrated in Figure 4.

**TABLE 2** Default parameter setting to run the soil–plant hydraulic and the stomatal model

| Parameter | Default value | Unit |
|-----------|---------------|------|
| $A_{max}$ | 38            | μmol m$^{-2}$s$^{-1}$ |
| $E$       | [0, 3 \cdot 10^{-3}] | cm$^3$s$^{-1}$ |
| $e_p$     | 2             | MPa |
| $e_A$     | 1             | μmol m$^{-2}$s$^{-1}$ |
| $g$       | 9.81          | m$^{-2}$ |
| $h$       | [−10, −20010] | cm |
| $h_r$     | −25           | cm |
| $k_m$     | 150           | mmol m$^{-2}$s$^{-1}$ |
| $k_s$     | $10^{-7}$     | cm$^3$s$^{-1}$hPa$^{-1}$ |
| $k_{sat}$ | $10^{-4}$     | cm$^{-1}$ |
| $k_{smax} (=k_s)$ | $10^{-7}$ | cm$^3$s$^{-1}$hPa$^{-1}$ |
| $L$       | 1000          | cm |
| $L_A$     | 0.02          | m$^2$ |
| $M_{Na,o}$ | $18.015 \cdot 10^{-3}$ | kg mol$^{-1}$ |
| $p_{atm}$ | 100           | kPa |
| $\Psi_{x}$ | −1.65        | MPa |
| $r_0$     | 0.05          | cm |
| $r_0$     | 1             | cm |
| $\rho$    | 2.6           | – |
| $\tau$    | 5             | – |
| VPD       | 1             | kPa |

Note: The numerical code to generate the figures of this study is openly available in figshare at https://doi.org/10.6084/m9.figshare.14540292.v4.

The plant parameters used in the soil–plant hydraulic model (e.g., leaf area, active root length, rhizosphere radius and root hydraulic conductance) are set in accordance with measurements of 4- to 5-week-old maize plants grown under laboratory conditions (Hayat et al., 2020) and are comparable to other studies (Abdalla et al., 2021; Cai et al., 2020; Meunier et al., 2018). Xylem vulnerability is parameterized according to measurements on corn varieties by Li et al. (2009). The minimum production and degradation rate of ABA is parameterized by $e_p$ and $e_A$, respectively. A sensitivity analysis of the stomatal steady-state solutions as a function of $e_p$ and $e_A$ is shown in Figure S1. To run the stomatal model and determine the stomatal steady-state solutions, maximum assimilation rate and Michaelis–Menten constant are deduced from gas exchange data under ambient CO$_2$ concentration (Yu et al., 2001).

3 | RESULTS

3.1 | Stomatal closure under soil and atmospheric drought

We first simulate soil–plant hydraulics and leaf gas exchange under default environmental conditions (sandy loam, VPD = 1 kPa) and obtain surfaces of $E_{leaf}(\Psi_{soil}, \Psi_{leaf})$, $g_s(\Psi_{soil}, \Psi_{leaf})$ and $A(\Psi_{soil}, \Psi_{leaf})$. Figure 5 shows the different flux variables ($E_{leaf}$, $g_s$, $A$) in relation to the leaf water potential and illustrates the hydraulically possible states at constant soil water potentials (grey soil isolines). Note that the leaf water potential at null transpiration, $\Psi_{leaf}(E = 0)$, is equal to $\Psi_{soil}$. We determine the SOL (red line) and run our stomatal model to obtain the stomatal steady-state solutions (blue lines). The model predicts steady-state transpiration rates (blue line, Figure 5a) that lie around the SOL. Even if at low soil water potential the predicted transpiration...
rate slightly crosses the SOL, our stomatal model prevents plants from moving too far into the non-linear zone.

### 3.2 | Stomatal responses to changing VPD

To understand the implications of atmospheric drought, we analyze our model at different VPDs. The left side of Figure 6 shows the stomatal steady-state solutions (blue lines) in response to changing VPDs. Solid, dashed and dotted lines in Figure 6.a,c,e refer to a VPD of 0.3, 1 and 3 kPa. All flux variables are illustrated in relation to the leaf water potential. For clarity, only the soil isoline (grey) at the highest soil water potential (wet soil) is shown. In addition, the SOL of each soil is illustrated in Figure 6.b. Under wet soil conditions, the hydraulic conductance of the soil is higher than the plant conductance. This can be seen from the stomatal steady-state solutions (blue lines) as they ‘start’ from the same point (\(g_s = 250 \text{ mmol m}^{-2}\text{s}^{-1}\) at \(-\Psi_{\text{leaf}} = -0.9 \text{ MPa}\)) for all three soils. The same applies to the SOLs (red) in Figure 6.b. Under well soil conditions, however, the shapes of the stomatal steady-state solutions and SOLs greatly differ between soils. Stomatal steady-state solutions bend rapidly towards very low \(g_s\) in sand, while stomatal closure is more gradual in loam. Therefore, the range of realized leaf water potentials is narrowed in sandy soils.

### 3.3 | Stomatal responses to changing soil properties

We further examine our model under different soil conditions and analyze the predicted stomatal closure as water supply conditions change. Figure 6.b,d,f shows the stomatal steady-state solutions (blue lines) in response to changing soil textures. Solid, dashed and dotted lines in Figure 6.b,d,f refer to a sandy loam, sand and loam, respectively. For clarity, only the soil isoline (grey) at the highest soil water potential (wet soil) is shown. In addition, the SOL of each soil is illustrated in Figure 6.b. Under wet soil conditions, the hydraulic conductance of the soil is higher than the plant conductance. This can be seen from the stomatal steady-state solutions (blue lines) as they ‘start’ from the same point (\(g_s = 250 \text{ mmol m}^{-2}\text{s}^{-1}\) at \(-\Psi_{\text{leaf}} = -0.9 \text{ MPa}\)) for all three soils. The same applies to the SOLs (red) in Figure 6.b. In drier soil conditions, however, the shapes of the stomatal steady-state solutions and SOLs greatly differ between soils. Stomatal steady-state solutions bend rapidly towards very low \(g_s\) in sand, while stomatal closure is more gradual in loam. Therefore, the range of realized leaf water potentials is narrowed in sandy soils.

### 4 | DISCUSSION

The proposed model of stomatal regulation results in adaptive stomatal behaviour for varying soils, climates and plant hydraulic traits. Stomata are predicted to close when the relation of assimilation rate and leaf water potential becomes non-linear. More precisely, stomata do not exceed the targeted steady-state solutions where the ratio of leaf water potential to assimilation rate (assumed to be proportional to the ABA level) is at a minimum. This allows stomata to prevent plants from critical water potentials without presupposing an optimization principle. The predicted stomatal closure depends on hydraulics and the relationship of assimilation to stomatal conductance \(A(g_s)\). We focus on the effects of soil properties and air moisture. Our analysis shows that in wet soils and low VPD, when water availability is not limiting, the non-linearity in \(A(\Psi_{\text{leaf}}, \Psi_{\text{leaf}})\) is controlled by \(A(g_s)\). In dry soils, when soil hydraulic conductivity limits the water supply, the non-linearity is controlled by soil–plant hydraulics.

Stomatal closure is predicted to be more abrupt in sandy soils, reflecting the steep decrease in hydraulic conductivity of coarse textured soils during drying. By contrast, stomatal closure in loamy soils...
is more gradual, since the decline in soil hydraulic conductivity is comparatively weak. High VPD exacerbates the effect of soil properties on stomatal closure by increasing evaporative demand and gradients in water potential around the roots. As a result, stomatal opening is generally favoured in well conductive soil and humid air conditions. In contrast, \( g_s \) is inhibited by low conductive soils and high VPD. Figure 7 shows stomatal conductance as fraction of an absolute maximum conductance \( (g_s \text{ max}) \) being a function of atmospheric (VPD) and soil \( (\Psi_{\text{soil}}) \) dryness. High values (close to one, blueish colours) indicate no or slight hydraulic limitation, low values (close to zero, reddish colours) indicate strong hydraulic limitation. Both VPD and soil drying cause stomatal closure. At high VPD, stomata close also in wet soils. At low VPD, stomata can fully open also in relatively dry soils. This result is qualitatively true for varying soil properties and plant traits. As shown for sandy loam, sand and loam, it varies quantitatively between different soil textures. For instance, the hydraulic limitations are more abrupt in sandy compared to loamy soils and the relative importance of the soil water status increases in coarse soil texture, which is expected for short-rooted plants, too. Overall, our model of stomatal regulation predicts stomatal closure during drought that is VPD and soil texture dependent.

For our stomatal model, we extend the hydraulic approach of Carminati and Javaux (2020) to a principle for regulating the stomata based on ABA dynamics. The model results in stomatal steady-state solutions and enables plants to avoid the hydraulic non-linearities that appear under high transpiration rates and in dry soils. In other words, our model allows plants to exploit the given water supply as long as extracting and transporting the soil water remains relatively comfortable. The resulting pattern of stomatal closure during drought is similar to what optimization models predict (Sperry et al., 2017;
STOMATAL CLOSURE DRIVEN BY NONLINEARITIES IN SOIL–PLANT HYDRAULICS

FIGURE 7 Filled contourplot showing VPD and soil water potential (Ψ\text{soil}) as major environmental constraints on leaf gas exchange expressing stomatal conductance (gs) as fraction of an absolute maximum (gs_max) of 450 mmol m^{-2}s^{-1} (cf. Chen et al., 2013) for a sandy loam (top), sand (centre) and loam soil (bottom). High values (close to one, blueish colours) indicate no or slight, low values (close to zero, reddish colours) indicate strong hydraulic limitation of stomatal conductance.

Wang et al., 2020). Yet the optimization models deliberately omit an underlying mechanism for the apparent stomatal behaviour. The novelty of our model approach is that it derives an optimal-like stomatal behaviour from ABA dynamics.

A key feature of the model is its adaptive behaviour to varying environmental conditions. For instance, rapid changes in evaporative demand (i.e., VPD) would pose a challenge to plants if they had to rely on a fixed relationship of gs and Ψ\text{c}. Thus, a fast and flexible stomatal regulation is beneficial to avoid cavitation and hydraulic disconnection from the soil. For this, stomatal regulation must match the time scale of the occurrence of water limitation. The typical reaction time of stomata is between minutes and hours (Vico et al., 2011) and matches well to the speed of extremely declining water potentials at the soil–root interface (Carminati & Javaux, 2020). ABA may indeed serve as suitable regulation mechanism on this time scale, provided it is synthesized de novo in leaves (Geiger et al., 2011; Sussmilch et al., 2017; Waadt et al., 2014). Although on the longer term plants have a broad range of drought responses (e.g., plant water storage, leaf shedding, control of cuticular transpiration and root to shoot ratio) (Choat et al., 2018; McAdam et al., 2016), stomatal closure remains the first and most effective measure to slow down plant dehydration (Choat et al., 2018).

Our model predicts stomatal closure that avoids plant dehydration under any hydraulic circumstance. In agreement with optimization models (cf. Anderegg & Venturas, 2020), we show that there is no fixed relationship between leaf water status and stomatal conductance. Furthermore, the adaptive stomatal safety mechanism allows plants to expand their ecological tolerance in response to soil and climatic conditions. In contrast to the notion of species-specific thresholds for stomatal closure and xylem vulnerability, our flexible model could enable the same genotype to thrive in highly contrasting soils and climates.

The main uncertainties of our model approach are associated with the ABA dynamics in plants. We focused on the hydroactive mechanism of stomatal movement since it is dominant in the largest plant phylogenetic group, the angiosperms (Brodribb & McAdam, 2017). Despite the continuous advances, there is still discussion about sites and dynamics of ABA production, transport and catabolism (Buckley, 2019). For instance, there is evidence that ABA production is triggered by decreasing leaf turgor rather than a decline in leaf water potential (Cardoso et al., 2020; McAdam & Brodribb, 2016; Pierce & Raschke, 1980). This could be easily integrated into our stomatal model and account for evidence of dynamic osmotic potential (Cardoso et al., 2020; Gersony et al., 2020). However, it would require additional parameters (i.e., the dynamics of osmotic potential), which are presumably species-specific and not readily available.

Our model relies on the limited evidence that ABA catabolism (and redistribution) is related to assimilation rate. Tallman (2004) provided an appealing theory to explain stomatal movements based on diurnal ABA fluctuations. Somehow in agreement with Tallman’s model, we predict maximum ABA levels during night. However, this is a speculative, albeit testable, hypothesis. Indeed, some experimental papers show contrary dynamics to what is assumed here (Dingkuhn et al., 1991; Jackson et al., 1995; Lee et al., 2006; Lovisolo et al., 2008; Qiu et al., 2017; Yang et al., 1993) while others are (partially) in line with the hypothesized time course of ABA (Corlett et al., 1998; Dingkuhn et al., 1991; Elamry & Hegazy, 1997; Haque et al., 2017; Jackson et al., 1995; Lovisolo et al., 2008; McAdam et al., 2011; Socias et al., 1997; Tardieu & Simonneau, 1998). Apparently, the literature seems inconclusive in this regard, underscoring the need for further experiments.

Moreover, our definition of [ABA] requires at least one offset to obtain realistic stomatal steady-state solutions (we included both ϵ_0...
changing environmental conditions. Finally, we see opportunities to other words, it predicts stomatal responses that are adaptive to physiology of stomatal regulation and rejects the notion that stomatal and catabolism. Rather than presupposing stomatal optimality, we explain optimal-like stomatal behaviour by drawing on insights from mechanism that prevents plants from critical water potentials. The model and catabolism. Thus, the model links soil transport have to be included.

To explicitly test the hypothesized algorithm of stomatal conditions should provide more evidence to the postulated stomatal non-linearity (Abdalla et al., 2021). For this, we present here an algorithm of stomatal movement, coordinated through time and space: Functional linkages between xylem and stomata, coordinated through time and space: Functional linkages and stomata, coordinated through time and space: Functional linkages non-linearity: Modelling stomatal conductance. We interpret \( \varepsilon_T \) and \( \varepsilon_A \) to be related to a minimum ABA production and degradation rate, respectively. In Figure S1, we show a sensitivity analysis of the stomatal steady-state solutions on both \( \varepsilon_T \) and \( \varepsilon_A \). We are aware that the mechanisms regulating stomatal movements are far more complex than what is assumed here. Yet we tried to keep our stomatal algorithm as simple as possible, which nevertheless contains ABA-mediated feedbacks and can be integrated into a hydraulic model without requiring too many parameters.

Although our analysis is purely theoretical and needs to be systematically proven, our proposed model is corroborated by existing observations. It predicts stomatal responses under varying environmental conditions in line with common observations of stomatal closure. For instance, four major environmental factors (holding other conditions constant) cause stomatal closure: (I) increasing VPD, (II) increasing CO2, (III) soil drought and (IV) reduced plant hydraulic conductance (Wang et al., 2020). Our model of stomatal regulation is consistent with all four responses: (I) Increasing VPD leads to an increase or saturation of \( E_\text{leaf} \) while stomata close and photosynthesis decreases (Figure 6a,c,e); (II) the effect of rising CO2 concentration causes transpiration and stomatal closure to decrease, while the assimilation rate increases due to a shift in the \( A(g_s) \) relation (Figure S2, left side); (III) loss of soil hydraulic conductivity causes \( E_\text{leaf} \), \( g_s \) and \( A \) to be down-regulated in drying soils (cf. the magnitude of leaf gas exchange reduction in Figures 5 and 6, and see the khaki-coloured area in Figure 1); and (IV) reduced plant hydraulic conductance causes leaf gas exchange to decrease already in wet soils (Figure S2, right side).

Modelling and experimental studies have indicated that stomata close at the onset of soil-plant hydraulic non-linearity (Abdalla et al., 2021; Carminati & Javava, 2020). For this, we present here an explaining mechanism based on the consideration that hydraulic and photosynthesis determine the non-linearities of \( A(g_\text{soil}, \Psi_\text{leaf}) \) to which the stomata presumably respond. Continuous measurements of \( \Psi_\text{soil}, g_\text{soil} \) and \( A \) on plants growing in varying soils and at varying atmospheric conditions should provide more evidence to the postulated stomatal behaviour. To explicitly test the hypothesized algorithm of stomatal regulation, measurements of [ABA], its production, degradation and transport have to be included.

In conclusion, our model of stomatal regulation proposes a mechanism that prevents plants from critical water potentials. The model explains stomatal closure during drought based on ABA biosynthesis and catabolism. Rather than presupposing stomatal optimality, we explain optimal-like stomatal behaviour by drawing on insights from stomatal physiology. Thus, the model links soil-plant hydraulicities to the physiology of stomatal regulation and rejects the notion that stomatal behaviour during drought can be appropriately modelled without the explicit consideration of soil-plant hydraulic properties. On the contrary, the model shows the strong dependence of stomatal responses on the hydraulic regime determined by soil, plant and atmosphere. In other words, it predicts stomatal responses that are adaptive to changing environmental conditions. Finally, we see opportunities to test our model on the leaf and plant scales and to apply it in ecosystem models.

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DATA AVAILABILITY STATEMENT
The numerical code to generate the figures of this study is openly available in figshare at https://doi.org/10.1084/m9.figshare.14540292.v4

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