

1           A Modeling Approach to Stomatal Conductance  
2           under Different Vapor Pressure Conditions

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18           **Abstract**

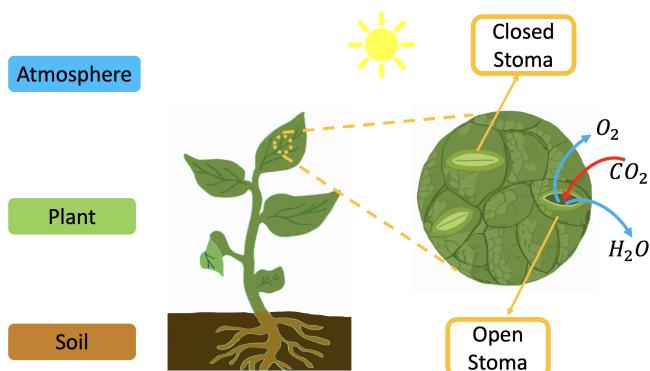
19           Stomatal conductance, determined by the stomatal aperture of leaves, governs  
20           gas exchange between plants and the atmosphere. This mechanism is closely  
21           related to photosynthesis and the ability of plants to adapt to environmental  
22           changes, including those caused by global warming. This study proposes a two-  
23           dimensional nonlinear model based on ordinary differential equations to estimate  
24           stomatal conductance over time. The model integrates key environmental drivers,  
25           air temperature and relative humidity, through the vapor pressure deficit, and  
26           couples stomatal conductance with leaf water content. A modified Gompertz-  
27           type equation captures the asymmetric and time-delayed response of stomatal  
28           conductance towards a dynamic steady-state target. We perform both local and  
29           global sensitivity analyses to assess parameter influence, revealing vapor pressure  
30           deficit as the most significant factor influencing stomatal effects. The findings  
31           indicate that the model effectively forecasts trends in stomatal conductance,

32 providing information on plant water status and their possible regulation under  
33 different environmental conditions.

34 **Keywords:** transpiration, vapor pressure deficit, gas exchange, soil-plant-atmosphere  
35 continuum, stomatal behavior, dynamical modeling, global warming

## 36 1 Introduction

37 Stomatal conductance ( $g_s$ ) governs the exchange of water vapor and carbon diox-  
38 ide between leaves and the atmosphere along the soil–plant–atmosphere continuum  
39 (SPAC) and, therefore, plays a central role in plant responses to drought, heat, and  
40 other stressors associated with global warming (GW) [1, 2]. Accurately represent-  
41 ing the temporal variability of  $g_s$  is essential for understanding how plants adjust to  
42 rapidly changing environmental conditions. Mediterranean-type climate regions, such  
43 as California, the Mediterranean Basin, South Africa, Australia, and Chile, are par-  
44 ticularly affected by GW as warmer and drier summers intensify water limitations for  
45 both natural and agricultural vegetation [3–6]. In these ecosystems,  $g_s$  is widely used  
46 as a physiological indicator of plant water status and adaptation capacity [7]. Figure 1  
47 illustrates the SPAC and the role of stomata in mediating gas exchange.



**Fig. 1** Schematic representation of gas exchange within the soil–plant–atmosphere continuum. Photosynthesis facilitates the entry of  $CO_2$  through open stomata, releasing oxygen ( $O_2$ ), while transpiration releases water vapor ( $H_2O$ ). (Source: Original Work).

48 Several modeling strategies have been developed to describe stomatal conductance.  
49 Empirical models, such as those of Jarvis [8] and Ball–Woodrow–Berry [9], relate  $g_s$   
50 to environmental variables or photosynthesis and often yield strong correlations with  
51 measurements [10]. Optimization models [11, 12] frame stomatal behavior as a trade-  
52 off between carbon assimilation and water loss, while mechanistic models incorporate  
53 hydraulic and chemical signaling pathways [13, 14]. More recently, dynamic approaches  
54 have been proposed to capture the short-term temporal response of  $g_s$  under changing  
55 environmental conditions. This type of approach includes coupled differential equation

systems that describe guard-cell processes [15], irradiance-driven stomatal responses [16], and models integrating solute dynamics, mesophyll water content, and water flow [17]. Despite these advances, many existing models assume steady-state behavior, require biophysical parameters that are difficult to measure, or do not explicitly link stomatal conductance with leaf water content ( $W$ ) in a tractable dynamic framework. These limitations reduce the applicability of current models under realistic environmental variability [2, 18].

To address this gap, the objective of this study is to develop and analyze a two-dimensional ordinary differential equation (ODE) model that explicitly couples the temporal evolution of stomatal conductance ( $g_s$ ) and leaf water content ( $W$ ). In our formulation,  $g_s$  evolves toward a steady-state target modulated by environmental drivers, represented through the parameter  $\delta_e$ , which corresponds to the vapor pressure deficit (VPD) and reflects the interaction between air temperature ( $T_a$ ) and relative humidity ( $RH$ ) [16, 19]. This structure provides a simplified yet physiologically grounded representation of stomatal dynamics.

The novelty of our approach lies in the following contributions: (i) introducing a reduced dynamic framework that links  $g_s$  and  $W$  in a physiologically interpretable manner; (ii) incorporating environmental variation through the parameter  $\delta_e$ , which reflects the interaction between air temperature and relative humidity; (iii) performing a sensitivity analysis to evaluate the influence of  $\delta_e$  on model trajectories; and (iv) assessing the model's robustness using experimental data through a cross-validation procedure. Together, these elements provide an efficient and interpretable tool for examining plant responses to environmental stressors, particularly under conditions intensified by GW in Mediterranean-type ecosystems.

This work is organized as follows. First, we present the complete two-dimensional system and the assumptions used to derive the model. Next, we perform a sensitivity analysis to assess the impact of  $\delta_e$  on model solutions. Finally, we evaluate the robustness of the model through a cross-validation procedure using experimental data. Additional qualitative properties of the system, including equilibrium analysis and stability, are presented in the Appendix.

## 2 Model Formulation

### 2.1 Leaf water content

Taking into account the approach presented in [17], we study how  $\delta_e$  influences the variation of leaf water content over time. The rate of change of  $W = W(t) > 0$  ( $mol\ m^{-2}$ ) varies over time (for notational simplicity, we omit the explicit time dependence of  $W$ ) according to inflows and outflows described by:

$$\frac{dW}{dt} = F_{in}(t) - F_{out}(t). \quad (1)$$

<sup>92</sup> The inflow  $F_{in}(t)$  is determined by the leaf water potential ( $\Psi_l < 0$ ) and the soil water  
<sup>93</sup> potential ( $\Psi_s < 0$ ). When  $\Psi_l$  is less than  $\Psi_s$ , water flows from the soil to the leaf:

$$F_{in}(t) = \frac{\Psi_s - \Psi_l}{R_{sl}}, \quad (2)$$

<sup>94</sup> where  $R_{sl} > 0$  ( $M\text{Pa mol}^{-1} m^2 s$ ) is the hydraulic resistance between the soil and the  
<sup>95</sup> leaf. The  $\Psi_l$  is determined by:

$$\Psi_l = P_l - \pi_l, \quad (3)$$

<sup>96</sup> where  $P_l \geq 0$  ( $M\text{Pa}$ ) and  $\pi_l > 0$  ( $M\text{Pa}$ ) represent the turgor pressure in the leaf and  
<sup>97</sup> the osmotic pressure in the leaf, respectively, both determined by  $W = W(t)$  (see [20]).  
<sup>98</sup> As  $W$  increases, cell expansion occurs, stretching the cell walls and thereby increasing  
<sup>99</sup>  $P_l$ . Conversely, a higher  $W$  leads to the dilution of osmotic solutes within the cells,  
<sup>100</sup> resulting in a decrease in  $\pi_l$ . From these considerations, the following equations are  
<sup>101</sup> derived:

$$\begin{aligned} P_l &= \pi_{lo} \cdot H(W) \\ \pi_l &= \pi_{lo} \cdot \frac{W_{max}}{W}, \end{aligned} \quad (4)$$

<sup>102</sup> where  $W_{max}$  ( $\text{mol m}^{-2}$ ) is the maximum leaf water content,  $\pi_{lo}$  ( $M\text{Pa}$ ) is the value  
<sup>103</sup> of  $\pi_l$  when  $W = W_{max}$ , and  $H(W)$  is the function defined as follows:

$$H(W) = \begin{cases} 0 & \text{if } W \leq W_{tlp} \\ \frac{W - W_{tlp}}{W_{max} - W_{tlp}} & \text{if } W > W_{tlp}, \end{cases} \quad (5)$$

<sup>104</sup> where  $W_{tlp}$  ( $\text{mol m}^{-2}$ ) represents the leaf water content at the turgor loss point (for  
<sup>105</sup> more details on the turgor loss point, see [21]).

<sup>106</sup> Thus, from (4) and (5), it is obtained that

$$\Psi_l = \pi_{lo} \left( H(W) - \frac{W_{max}}{W} \right), \quad (6)$$

<sup>107</sup> and, consequently, the inflow is determined by

$$F_{in}(t) = \frac{1}{R_{sl}} \cdot \left[ \Psi_s - \pi_{lo} \cdot \left( H(W) - \frac{W_{max}}{W} \right) \right]. \quad (7)$$

<sup>108</sup> On the other hand,  $F_{out}(t)$  is determined by the transpiration rate ( $E$ ,  
<sup>109</sup> ( $\text{mol H}_2\text{O m}^{-2}$ )) according to the equation:

$$E = \left( \frac{g_s}{1 + r_b \cdot g_s} \right) \cdot \frac{\delta_e}{p_{atm}}. \quad (8)$$

<sup>110</sup> As shown in [22, 23],  $p_{atm}$  represents the atmospheric pressure ( $M\text{Pa}$ ),  $r_b$   
<sup>111</sup> ( $(\text{mol m}^{-2} \text{s}^{-1})^{-1}$ ) represents the boundary layer resistance and  $\delta_e$  ( $M\text{Pa}$ ) is defined