Optimal stomatal behavior with competition for water and risk of hydraulic impairment

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For over 40 y the dominant theory of stomatal behavior has been that plants should open stomates until the carbon gained by an infinitesimal additional opening balances the additional water lost times a water price that is constant at least over short periods. This theory has persisted because of its remarkable success in explaining strongly supported simple empirical models of stomatal conductance, even though we have also known for over 40 y that the theory is not consistent with competition among plants for water. We develop an alternative theory in which plants maximize carbon gain without pricing water loss and also add two features to both this and the classical theory, which are strongly supported by empirical evidence: (i) water flow through xylem that is progressively impaired as xylem water potential drops and (ii) fitness or carbon costs associated with low water potentials caused by a variety of mechanisms, including xylem damage repair. We show that our alternative carbon-maximization optimization is consistent with plant competition because it yields an evolutionary stable strategy (ESS)—species with the ESS stomatal behavior that will outcompete all others. We further show that, like the classical theory, the alternative theory also explains the functional forms of empirical stomatal models. We derive ways to test between the alternative optimization criteria by introducing a metric—the marginal xylem tension efficiency, which quantifies the amount of photosynthesis a plant will forego from opening stomatal an infinitesimal amount more to avoid a drop in water potential.

biosphere–atmosphere feedbacks | carbon cycle | embolism | hydraulic vulnerability

Stomata are openings in plant leaves that determine the rate of water loss and photosynthetic carbon gain by plants. The importance of stomata and the basic mechanics of what they do have been known for well over a century (1). Stomatal aperture increases with increased humidity and light, decreases with increased CO_2 (2), and decreases with desiccation (3). Most fundamentally, stomatal conductance is correlated with photosynthesis (4). Because mechanistic understanding of stomatal function is incomplete, all current ecosystem and Earth system models use empirical equations to capture the observed relationships between stomatal conductance and environmental drivers (2, 5). As a result, theories of stomatal behavior based on maximizing evolutionary fitness are critical to help avoid the risks of out-of-sample prediction inherent in empirical models (6–8).

The preeminent theory of the adaptive value of stomatal behavior is that stomatal aperture should be regulated to keep marginal water use efficiency constant, at least over short periods of time:

$$\lambda = \frac{\partial A / \partial g_s}{\partial E / \partial g_s}. \qquad [1]$$

This stipulates that the benefit of increased photosynthetic rate (A) caused by a small increase in stomatal conductance to water vapor (g_s) should always equal the corresponding cost of increased evaporative water loss (E) times the carbon price of water (λ) [henceforth the water use efficiency hypothesis (WUEH)]. Eq. **1** was originally derived by Cowan and Farquhar (6) (henceforth

CF77) in a seminal study of a simple model. Plants were assumed to evolve to maximize carbon gain in a fluctuating environment subject to the constraint of a fixed amount of available water:

$$\max_{g_s} \int A dt$$

$$\text{subject to} \int E dt \leq b.$$

Constrained optimization problems like the one above are conventionally solved using a Lagrangian multiplier (λ), which in this case is the amount that carbon gain would increase if the constraint were relaxed. Note that the original CF77 formulation (6) used the inverted version of the fraction (i.e., $\lambda = \partial E / \partial A$), but we use the more ecologically intuitive $\lambda = \partial A / \partial E$ described by ref. 9 here.

For nearly 40 y, the WUEH has been the dominant explanation of why stomata behave the way they do (7, 8, 10–14), primarily because of its remarkable success in explaining empirical data from many species, biomes, and environments (14–27). The hypothesis often works in contexts far removed from the assumptions of the simple model in CF77 (6), which includes no competition for water or hydraulic impairment from low plant water potentials. For this reason, Eq. **1** is most appropriately viewed as a stand-alone hypothesis whose validity does not depend on restrictive assumptions behind any published optimization model, including the one in CF77 (6). Moreover, a rich theoretical literature (7–9, 14, 28–33) shows that the optimal stomatal

Significance

Plants lose water and take up carbon through stomata, whose behavior has major influences on global carbon and water fluxes. Yet both competition for water and the potential fitness costs of hydraulic damage during water stress could alter how stomata behave. Here, we add variable xylem conductivity to water and carbon costs of low-xylem water potentials to the classic stomatal optimization and a pure carbon-maximization optimization. We show that both optimizations can reproduce known stomatal responses to environmental conditions but that the pure carbon-maximization optimization is also consistent with competition for water. We describe a new measure—the marginal xylem tension efficiency—that can be used to test stomatal optimizations.

behavior predicted by Eq. **1**, when applied to biophysical models of photosynthesis and transpiration, closely matches the functional forms of empirical stomatal models, which themselves have extraordinary empirical support (2, 5, 7, 27, 34). For this reason, the WUEH is widely used to guard against out-of-sample behavior in the novel climates created in ecosystem models (35–39). Finally, several notable efforts have been made to extend WUEH to situations including soil moisture stress (11, 12, 28, 33, 40–42) and competition (43) and to develop a theory of the value of λ over the short time scales during which it should be approximately constant and how λ should change over weeks, months, or seasons (9, 11, 12, 28, 32). However, a priori prediction of the value of λ remains challenging and no modeling study has to our knowledge shown whether or not Eq. **1** predicts the observed Weibull-like relationship between stomatal aperture and leaf water potential (Fig. 1).

Despite all of the empirical support and explanatory power, the WUEH has always been perplexing to community ecologists, because fundamentally, it makes sense for a plant to close stomates and forgo photosynthetic carbon gain only if the water it saves can be used later when conditions favor a higher ratio of carbon gain to water loss. But widespread evidence reveals that plants episodically compete for limited water in most locations and that root systems of neighboring plants overlap substantially (44–46). Roots commonly extend to three times a plant's crown radius or more (44–46). As first pointed out by Cohen (ref. 47, p. 51), "The selective advantage of a high efficiency of water utilization for photosynthesis depends on the degree to which the water in the soil occupied by the roots of a single plant can be used by that plant alone, and cannot escape unused. This is because the highest efficiency necessarily means a slower growth rate. If the water in the soil can be removed by other plants which utilize it less efficiently, but grow more quickly, then these plants will have a selective advantage over an efficient, slow-growing plant."

Cohen's point is that, because plants can steal each other's water, game theoretic methods are needed to solve correctly for a competitive optimum—a stomatal strategy that will competitively exclude all others. Cowan (43) also made this point in a prescient early paper, in which he contrasted a game-theoretic optimization with a noncompetitive optimization. However, he illustrated only the most tentative first step—the difference between one plant in a patch and two sharing a patch twice as large. In the noncompetitive optimizations in the vast majority

of the WUEH literature, the optimal strategy is found either by ignoring competing plants (i.e., a plant in a pot) or by assuming that all plants share the same stomatal algorithm (i.e., simultaneous optimization of all competing plants in a population). In contrast, a competitive optimum or evolutionary stable strategy (ESS) (48) is explicitly solved for as the strategy that can invade a monoculture of any other strategy and that cannot be invaded by any other strategy when it is itself in monoculture (48). Because the ESS is the strategy that can competitively exclude all others, it is the expected outcome of evolution in the presence of competition for water. Theoretical and empirical studies have demonstrated large differences between competitive and noncompetitive optima, including studies of plants competing for water.

In this paper, we derive the ESS stomatal algorithm for a class of completion models and show that it simply maximizes net carbon gain at every instant in time without explicitly pricing water loss [henceforth the simple carbon-maximization hypothesis (CMH)]. As in the WUEH, the benefit of opening stomata in the CMH is increased photosynthesis. Because the photosynthetic rate increases monotonically with stomatal aperture, the CMH predicts wide-open stomates in the absence of direct carbon costs, like those that have been added to some WUEH models (29). In particular, the literature on xylem embolism and/or cavitation induced by hydraulic stress details a compelling suite of associated fitness costs of low water potentials (49–51). Studies have uncovered at least three carbon costs associated with low xylem potentials: (*i*) a direct cost of refilling embolized vessels when this is possible (52–54), (*ii*) an indirect cost of reduced current photosynthesis due to partial desiccation (42, 55), and (*iii*) an opportunity cost of reduced future photosynthesis caused by reduced water supply to stomates when xylem damage cannot be completely repaired, which induces a persistent restriction of stomata and limits the supply of CO_2 for photosynthesis (56–59). We note that this cost function could include some negative costs (i.e., benefits); for example, low water potential driven by high evapotranspiration could reduce the carbon cost of acquiring water by increasing the water flow rate per unit xylem (29, 60). Finally, the ultimate opportunity cost is experienced by plants with severe xylem damage, which leads to death and the loss of all future carbon and fitness gains (61–63).
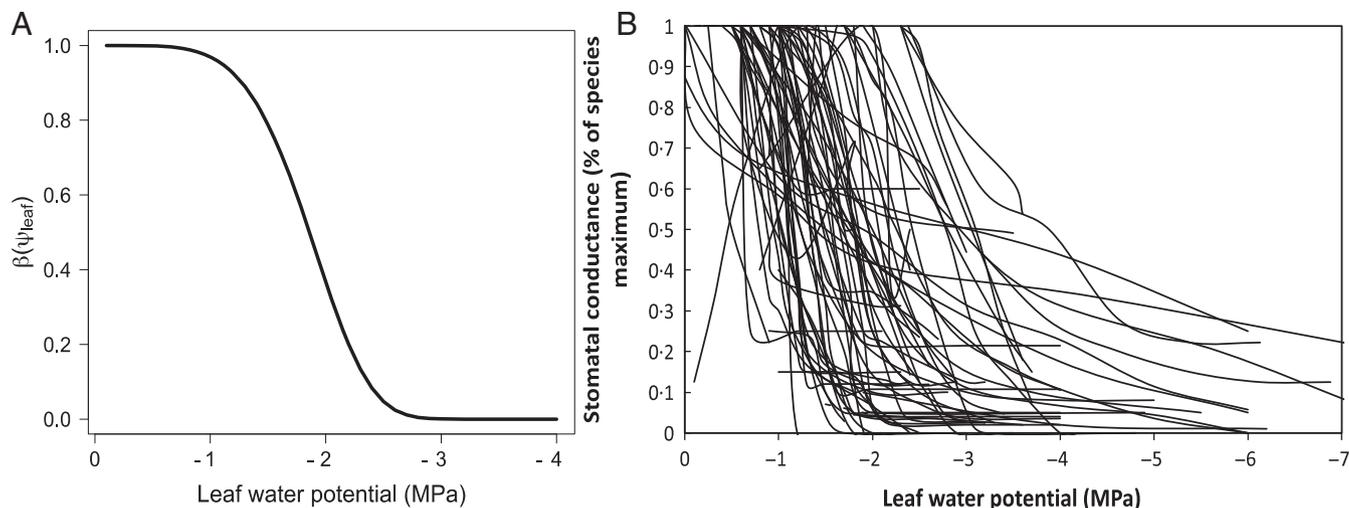

Fig. 1. (*A*) Stomatal conductance response as a function of leaf water potential [$\beta(\psi_{leaf})$] with a Weibull-like functional form. (*B*) Observed stomatal conductance response (normalized to species-level maximum) as a function of leaf water potential (MPa) from 70 woody plant species from around the globe Reprinted with permission from ref. 82.

Mathematically, the CMH optimization criterion is

$$\frac{\partial A}{\partial g_s} - \frac{\partial \Theta}{\partial g_s} = 0, \qquad [2]$$

where Θ is the sum of the direct carbon costs associated with low xylem potentials. To provide a thorough comparison of the CMH and the WUEH, we consider models with all possible combinations of the following: (*i*) the alternative optimization criteria (Eq. 1 vs. Eq. 2), (*ii*) with and without carbon costs associated with low xylem potentials, and (*iii*) with and without variable xylem conductivity caused by embolism and/or cavitation. We do not believe that all of these combinations are equally realistic or justifiable. In particular, knowledge of the large costs associated with low xylem potential, which was obtained after 1977, might have obviated the need for the assumption of a fixed water supply in CF77 (6). On the other hand, WUEH is widely applied where such costs are thought to be high, as in ecosystem models under climate change (35–39). We include all combinations of *i–iii* simply to explore the impact of each component on the predicted stomatal behavior and in recognition of the fact that Eq. 1 is best viewed as a stand-alone hypothesis because of its widespread use. For each combination, we derive the optimal stomatal algorithm and compare its functional form to that of published empirical models and to the conductance-potential relationship in Fig. 1. We also derive a criterion that should be particularly useful in separating the CMH and WUEH optimization criteria with empirical data—the marginal xylem tension efficiency, which is the photosynthetic carbon that a competitively optimal plant forgoes to avoid the incremental costs associated with reduced water potentials (see below). The results show that the CMH is as good as the WUEH at predicting the functional forms of empirical stomatal models, but more robustly predicts observed responses of stomates to low water potentials.

The Model

We first describe the equations necessary to predict plant water use and carbon gain, except for the algorithm that regulates stomates. Consider a plant with leaf area, area$_L$, and fine root area, area$_R$, and assume for simplicity that all leaves experience the same environmental inputs $\mathbf{I_E} = (R_l, R_s, \text{PAR}, w_a, T_a, s_w, C_a)$, or, respectively, (per unit leaf area absorbed long-wavelength radiation, short wavelength radiation, and photosynthetically active radiation, moles water vapor per unit of air volume, air temperature, wind speed, and the atmospheric concentration of CO_2), and that all fine roots experience the same soil water potential, ψ_s. The six unknown state variables of the plant are C_i, the internal concentration of CO_2 in the leaves; T_L, the leaf temperature; A_N, the net rate of photosynthesis minus respiration per unit leaf area; E, the transpiration rate per unit leaf area; ψ_L, the water potential inside the leaf; and g_s, the stomatal conductance.

We assume the classic model of photosynthetic CO_2 demand (64),

$$A_N = \text{Min}\left[\frac{J}{4}\frac{C_i - \Gamma^*}{C_i + 2\Gamma^*}, V\frac{C_i - \Gamma^*}{C_i + k}\right] - R, \qquad [3]$$

where Γ^*, k, V, and the respiration rate R are functions that depend on leaf temperature, and J, the potential electron transport rate, is a function of PAR. Diffusive supply of CO_2 is modeled as

$$A_N = \frac{g_s g_b(s_w)}{1.6\left(\frac{1.37}{1.6}g_s + g_b(s_w)\right)}(C_a - C_i), \qquad [4]$$

where $g_b(s_w)$ is the wind-speed-dependent leaf boundary layer conductance to water vapor. Leaf temperature is given by the familiar energy balance,

$$R_l(T_a) + R_s = \varepsilon \sigma_B T_L^4 + \Lambda E + \phi(s_w)(T_L - T_a), \qquad [5]$$

where ε is leaf emissivity (typically 0.94–0.95), σ_B is the Boltzmann constant, Λ is the latent heat of evaporation, and $\phi(s_w)$ is the wind speed-dependent proportionality of forced heat convection. Water loss per unit leaf area is

$$E = \frac{g_s g_b(s_w)}{g_s + g_b(s_w)}[w^*(T_L) - w_a], \qquad [6]$$

where $w^*(T_L)$ is the water content of saturated air at temperature T_L (moles water per mole of air).

Evaporation given by **[6]** must be balanced by water supplied to the leaves. When the hydraulic conductance (K) of a pipe is constant, Darcy's law is used to model flow rates in response to a potential gradient. However, when K varies with water potential (ψ) itself, hydraulic supply is modeled using the Kirschoff transform, by integrating the hydraulic conductance K from one end of a continuum (ψ_1) to the other (ψ_2) (65): Flow = $\int_{\psi_2}^{\psi_1} K(\psi)d\psi$. The conductivity of xylem, $K(\psi)$, decreases as water potential falls because elements embolize and/or cavitate, which prevents the flow of water through them. A good empirical functional form of the fall in conductivity is the Weibull function (Fig. 1).

Because water supply must equal demand (assuming negligible change in the amount of water in the xylem, e.g., plants with limited capacitance or timescales longer than the capacitance time constants for plants),

$$\text{area}_L E = \rho \ \text{area}_R \int_{\psi_L}^{\psi_s} K(\psi)d\psi, \qquad [7]$$

where ρ is a conductivity from soil to the fine-root xylem and ψ_L is leaf water potential. We can combine the above equation with **[6]** to produce

$$\frac{\rho \ \text{area}_R}{\text{area}_L}\int_{\psi_L}^{\psi_s} K(\psi)d\psi = \frac{g_s g_b(s_w)}{g_s + g_b(s_w)}[w^*(T_L) - w_a],$$

which physically connects loss of xylem conductivity [nonconstant conductivity on the left-hand side (LHS)] to stomatal conductance on the right hand-side (RHS). For example, a drop in stomatal conductance on the RHS requires an increase in ψ_L on the LHS for the equation to balance and thus an increase in $K(\psi_L)$. In what follows, we define $K_{\max} \equiv \frac{\rho \ \text{area}_R}{\text{area}_L}K(0)$.

Finally, we define $\Theta(\psi_L)$ as the carbon cost per unit time associated with leaf xylem potential ψ_L (i.e., the carbon costs of hydraulic damage) and thus the total rate of carbon gain is

$$C_{\text{gain}} = A_N - \Theta(\psi_L). \qquad [8]$$

Because costs accelerate as ψ_L falls, we assume that $\Theta(\psi_L)$ is a concave-up function, so that $d\Theta(\psi_L)/d\psi_L < 0$ (damages grow as water potential drops) and $d^2\Theta(\psi_L)/d\psi_L^2 > 0$. Note that this excludes the possibility that negative costs (29, 50) might dominate over some portion of the range of ψ_L variation. Finally, we define $\theta_{\min} \equiv \Theta(0)$.

As written, Eq. **8** strictly applies only to the case in which carbon costs are instantaneous and depend only on current environmental inputs (i.e., vapor pressure deficit, soil water potential, temperature, down-welling short- and long-wavelength radiation, and wind speed). This restriction technically excludes important phenomena such as permanent loss of xylem hydraulic conductivity. However, we can probably obtain some insight about severe damages and costs associated with very low xylem

potentials because the cost function is concave-up. The assumption of temporally dependent costs must be analyzed as a full nonlinear stochastic optimization problem, which will require separate treatment.

The six Eqs. **3–8** have seven unknowns (C_i, T_L, A_N, E, ψ_L, C_{gain}, and g_s), and so we need an additional equation to close the system. The seventh equation is taken either from the WUEH,

$$\frac{\frac{\partial C_{\text{gain}}}{\partial g_s}}{\frac{\partial E}{\partial g_s}} = \lambda, \qquad [9]$$

or from the CMH,

$$\frac{\partial C_{\text{gain}}}{\partial g_s} = 0. \qquad [10]$$

We now show that **[10]** specifies a competitive optimum. Specifically, we propose that if carbon gain is monotonically related to fitness and the water commons are large enough so that a rare strategy has negligible impact on water availability, then the stomatal algorithm that maximizes carbon gain under every possible set of environmental conditions (every possible value of $\mathbf{I_E}$ and ψ_s) will competitively exclude all others and thus be the ESS (48). This proposition is easily proved both for simple population dynamic models in which water is the only resource limited by plant consumption (i.e., ref. 66) and for age- and size-structured forest models of competition for light and water, with and without stochastic rainfall (i.e., refs. 67, 68). We assume that water is equally accessible to a large number of plants (i.e., all plants experience the same ψ_s) because of the wide overlap of root systems, so that any one plant's water use has negligible impact on its future supply (although collective water use by all of the plants may still affect future supply).

Now consider the simplest case in which all plants in a population are identical and both $\mathbf{I_E}$ and precipitation are constant. The fitness of a plant in this population (W), in units of per capita lifetime reproductive success, is a function of its rate of carbon gain (C_{gain} from Eq. **8**). A solution of the system of Eqs. **3–8** implicitly defines C_{gain} as a function of g_s and the environmental inputs ψ_s and $\mathbf{I_E}$, which we write as $C_{\text{gain}}(g_s, \psi_s, \mathbf{I_E})$. Thus, the fitness is $W(C_{\text{gain}}(g_{sR}, \psi_s, \mathbf{I_E}))$ or, to simplify the notation, $W(g_{sR}, \psi_s, \mathbf{I_E})$, where the subscript "$R$" signifies the stomatal algorithm of the "resident" type. At population dynamic equilibrium of a monoecious monoculture of the resident, $W(g_{sR}, \psi_{sR}*, \mathbf{I_E}) = 1$, where $\psi_{sR}*$ signifies soil water potential at population dynamic and hydrological equilibrium (because expected lifetime reproductive success equals one at population dynamic equilibrium). We now consider a second invading species with stomatal conductance g_{sI}, which is so rare that it has negligible impact on the soil water potential. Invasion will succeed if its fitness is greater than one, $W(g_{sI}, \psi_{sR}*, \mathbf{I_E}) > 1$, and fail if its fitness is less than one. If fitness is monotonically related to carbon, then the stomatal algorithm that instantaneously maximizes carbon gain under all environmental conditions will successfully invade because it must gain more carbon than the suboptimal resident and thus have fitness higher than the resident's fitness of one. Similarly, invasion will fail if the resident has the carbon-maximizing stomatal algorithm because the suboptimal invader's fitness must then be less than the resident fitness, which is one. We solve for the carbon-maximizing strategy by differentiating carbon gain with respect to stomatal conductance and then setting the result equal to zero, as in Eq. **10**. This method strictly finds local competitive optima, which cannot be invaded by any sufficiently similar stomatal algorithm (because of the possibility of two or more local optima).

It is important to understand that our results require the assumption that plants compete for a common pool of water. If each plant had a portion of the water for its sole use, then instantaneous maximization of carbon gain would cause the plant to deplete its limiting water during periods of low photosynthetic return, rather than to save it for more favorable conditions. We conjecture that the WUEH's predictions would be the ESS if plants could not steal each other's water.

Mathematical Analysis

Collectively, Eqs. **7–10** add three features to classical models: two alternative optimization criteria, conductivity that decreases with water potential $K(\psi_L)$, and direct carbon cost of low water potentials $\Theta(\psi_L)$. To uncover the separate effect of each addition, we derive results for eight different cases consisting of all possible combinations of the WEUH vs. CMH optimization criterion, Weibull $K(\psi_L)$ vs. constant $K(\psi_L) = K_{\text{max}}$ and concave-up $\Theta(\psi_L)$ vs. constant $\Theta(\psi_L) = \Theta_{\text{min}}$ (first four columns of Table 1). In Table 1 and in text below, we use the shorthand $\Theta'(\psi_L)$ for the derivative of Θ with respect to ψ_L.

We now define a quantity that should prove useful in future studies that attempt to test between the alternative optimization criteria (9, 10) with data. Let the "marginal xylem tension efficiency" (MXTE) be

$$\text{MXTE} = \frac{\frac{\partial A_N}{\partial g_s}}{\frac{\partial(-\psi_L)}{\partial g_s}}. \qquad [11]$$

The numerator of the RHS of **[11]** is the amount of photosynthetic carbon that would be gained if the plant were to open its stomates by a small increment. One can think of this as the photosynthetic carbon that a competitively optimal plant forgoes to avoid the incremental costs associated with reduced water potentials and/or water loss. The denominator of the RHS gives the increase in leaf xylem tension (minus water potential) caused by the same small additional opening of stomates. Thus, the ratio of the two terms on the RHS is the photosynthetic carbon that the ESS is willing to forfeit to avoid a unit increase in xylem tension.

Using Eq. **8**,

$$\frac{\partial C_{\text{gain}}}{\partial g_s} = \frac{\partial A_N}{\partial g_s} - \frac{\partial \Theta}{\partial g_s} = \frac{\partial A_N}{\partial g_s} - \Theta'(\psi_L)\frac{\partial \psi_L}{\partial g_s}, \qquad [12]$$

and using Eq. **7**,

$$\frac{\partial E}{\partial g_s} = -\frac{\rho\ \text{area}_R}{\text{area}_L}K(\psi_L)\frac{\partial \psi_L}{\partial g_s}. \qquad [13]$$

Eqs. **9–13** lead immediately to the formulas for the MXTE in the eight cases in Table 1 (column 6). Note that the CMH MXTE in case 4 is a monotonically decreasing function of ψ_L, whereas the WUEH MXTE in case 8 is an increasing function of ψ_L if λ is sufficiently large and a decreasing function of ψ_L if λ is sufficiently small (Fig. 2B, dark blue line). The MXTE also increases as ψ_L decreases in cases 3, 4, and 7; is constant in case 5; and decreases as ψ_L decreases in case 6 (Fig. 2B). Together, these results show the following:

i) Variable xylem conductivity pushes the MXTE to decrease with ψ_L under the WUEH but has no effect on the MXTE under the CMH.

ii) Concave-up $\Theta(\psi_L)$ pushes the MXTE to increase as ψ_L decreases under both the WUEH and the CMH.

iii) Both cases 4 and 8 can predict that the MXTE will increase as ψ_L decreases if λ is sufficiently small in case 8 (Fig. 2B, dark blue dashed line). This, however, means that the calculation is dominated by changes in the marginal carbon cost of low water potential rather than by the plant's carbon price

Table 1. Mathematical results

Case	Optimization	Variable conductivity?	Carbon cost increases as ψ_L decreases?	$\beta(\psi_L)=$	MXTE
1	CMH	N	N	NA	NA
2	CMH	Y	N	NA	NA
3	CMH	N	Y	$\sqrt{\dfrac{K_{max}}{-\Theta'(\psi_L)}}$	$-\Theta'(\psi_L)$
4	CMH	Y	Y	$\sqrt{\dfrac{K(\psi_L)}{-\Theta'(\psi_L)}}$	$-\Theta'(\psi_L)$
5	WUEH	N	N	$\lambda^{-(1/2)}$	λK_{max}
6	WUEH	Y	N	$\lambda^{-(1/2)}$	$\lambda K(\psi_L)$
7	WUEH	N	Y	$\sqrt{\dfrac{K_{max}}{\lambda K_{max}-\Theta'(\psi_L)}}$	$\lambda K_{max}-\Theta'(\psi_L)$
8	WUEH	Y	Y	$\sqrt{\dfrac{K(\psi_L)}{\lambda K(\psi_L)-\Theta'(\psi_L)}}$	$\lambda K(\psi_L)-\Theta'(\psi_L)$

Optimization column: CMH means net carbon gain maximization; WUEH means the constant marginal water use efficiency hypothesis. Variable conductivity column: Y means that $K(\psi_L)$ decreases with ψ_L (empirically as a Weibull function); N means that $K(\psi_L)$ is equal to the constant K_{max}. Carbon cost Increases as ψ_L decreases column: Y means that the derivative of the cost function $\Theta'(\psi_L)$ increases as ψ_L decreases, which implies that the cost function itself is concave-up; N means that the cost function is constant (or zero) so that its derivative is zero. $\beta(\psi_L)=$ column: The optimal stomatal conductance (g_s^{opt}) in cases 3–8 is approximately proportional to $\frac{A_N\beta(\psi_L)}{\sqrt{\text{saturation deficit}}\sqrt{C_a-\Gamma}}$ in the special case in which $T_L \sim T_a$ and photosynthesis is carbon or light limited (see text). Recall that $\beta(\psi_L)$ is the stomatal sensitivity to leaf water potential. NA means "not applicable" because there is no internal optimum in cases 1 and 2. Instead, stomates are predicted to be always wide open in these cases. MXTE column: The MXTE is defined as $\text{MXTE} = \frac{\partial A_N}{\partial g_s}/-\frac{\partial \psi_L}{\partial g_s}$.

for water loss, in which case plants in case 8 approximately maximize instantaneous carbon gain.

iv) If λ is sufficiently large, then the WUEH implies in cases 6 and 8 that the MXTE will decrease with ψ_L whereas the CMH implies in cases 3 and 4 that it will increase as ψ_L decreases.

A second criterion that could be used to test between the alternative optimization criteria is λ itself, which most papers in the WUEH literature state should be constant over short periods, such as 1 d (11, 43). Using Eqs. 9, 10, and 13, we find that the CMH predicts instead that

$$\lambda = -\Theta'(\psi_L)\frac{1}{K(\psi_L)}\frac{1}{\rho}\frac{\text{area}_L}{\text{area}_R}. \qquad [14]$$

The RHS of [14] is a strongly concave-up increasing function of xylem tension if the conductivity function is a Weibull function. Eq. 14 reveals that a competitively optimal plant should adjust its marginal water use efficiency as xylem tension changes over all time scales. Constant λ over short time scales will generally be competitively suboptimal unless $\Theta'(\psi_L)\frac{1}{K(\psi_L)}$ is approximately constant, as would occur for example if $\Theta(\psi_L)$ were linear at low xylem tension (ψ_L near 0) where the Weibull function is often flat.

Although it is difficult to obtain closed-form solutions for the optimal stomatal conductance in the general case with either optimization criterion, we can do so for the useful special case of windy conditions in which $T_{\text{leaf}} \approx T_a$ and boundary conductance ($g_b(s_w)$) is approximately infinite. To keep the notation as simple as possible, we omit the leaf temperature dependence in the parameters in Eqs. 3 and 6 and set the conductivity units in Eq. 7 so that $\frac{\rho\,\text{area}_R}{\text{area}_L}=1$. We assume that leaves are in full sun and so are CO_2 limited, although it is easy to derive conditions for light-limited leaves simply by substituting $J/4$ for V and Γ^* for k.

The calculations in *SI Appendix 1* show that the optimal stomatal conductance is approximately

$$g_s^{opt} \approx \sqrt{\left[\frac{1.6}{C_a-\Gamma}\right]}\frac{A_N\beta(\psi_L)}{\sqrt{w^*-w_a}}, \qquad [15]$$

where Γ is the CO_2 compensation point, $\frac{V\Gamma^*+kR}{V-R}$, and with $\beta(\psi_L)$ in the various cases given by the fifth column in Table 1. This

$\beta(\psi_L)$ function explicitly represents the stomatal response to leaf water potential, has been widely observed, and should be thought of as a hydraulic shutoff valve on stomatal conductance (see below). Except for the beta function, Eq. 15 is remarkably similar to the empirical stomatal conductance models of Ball et al. (2), Leuning (5), and many others, with g_s proportional to A_N and inversely depending on saturation deficit and atmospheric CO_2. Moreover, the functional form of [15], except for the beta function, is the same under both optimization criteria. This result implies that the CMH is as good as the WUEH at predicting observed effects of photosynthetic rate, atmospheric CO_2, and saturation deficit on stomatal conductance.

The dependence on the square roots of CO_2 and the saturation deficit are not standard in the early empirical models, but inverse dependence on the square root of the saturation deficit is consistent with the available data (7, 26, 27) and has been shown previously to be approximately optimal under the WUEH (7). The square-root dependence for CO_2 has also been derived before in the WUEH literature, and we get very similar quantitative predictions if we substitute the CO_2 dependence in the Leuning

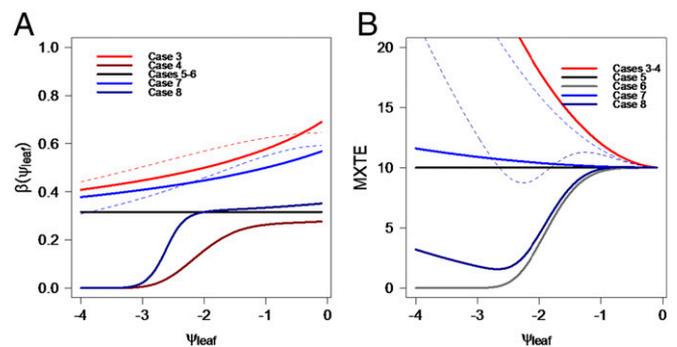**Fig. 2.** (*A*) Beta function (unitless) of stomatal sensitivity to leaf water potential across cases 3–8 described in Table 1. Note that *y*-axis values are arbitrary and were chosen to maximize visibility of the functional forms. (*B*) MXTE in response to changing leaf water potential across cases 3–8 in Table 1. Note that dashed lines indicate highly concave-up cost functions compared with the base scenario in a given case.
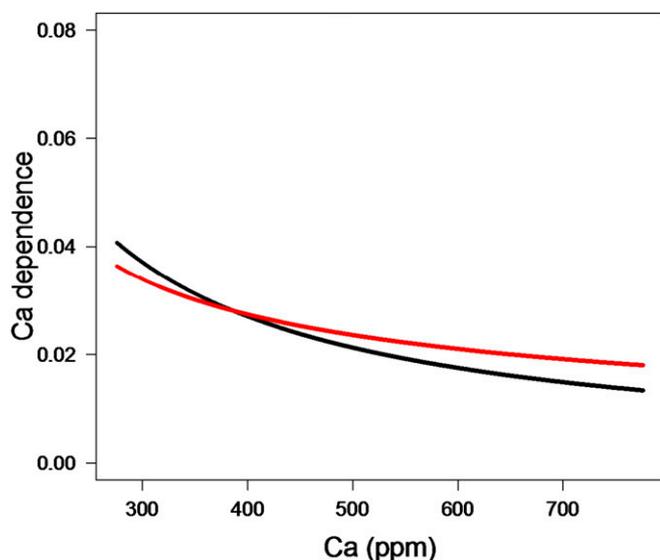
Fig. 3. Predictions of the CO_2 dependence as a function of varying atmospheric CO_2 concentrations (C_a; ppm) with the classic formulation $\frac{g_{max}}{C_a-\Gamma}$ (black) or the square-root dependence $\sqrt{\frac{1}{C_a-\Gamma}}$ (red) derived here, normalized at 380 ppm (because the empirical models that use the classic formulation contain the fitted constant g_{max}).

model: $\frac{g_{max}}{C_a-\Gamma}$, where g_{max} is a fitted constant, for $\sqrt{\frac{1.6}{C_a-\Gamma}}$ (Fig. 3). An alternative approximation for g_s^{opt} can be obtained by repeating the derivation in Medlyn et al. (7) for leaves in full sun and after adding variable conductivity and the carbon cost of low xylem potential:

$$g_s^{opt} \approx \frac{\sqrt{1.6(k+\Gamma)}}{C_a}\frac{A_N\beta(\psi_L)}{\sqrt{w^*-w_a}}. \qquad [16]$$

Eq. **16** has precisely the same beta functions as [15] in all eight cases. Note that this approximation predicts that conductance is inversely proportional to C_a rather than the square root of C_a minus a constant. However, plots comparing $\frac{\sqrt{k+\Gamma}}{C_a}$ in Eq. **16** and $\sqrt{\frac{1}{C_a-\Gamma}}$ from Eq. **15** show that they are quantitatively similar. Moreover, [15] appears to be the more accurate of the two approximations for the situation considered here.

The most unique feature of [15] and [16] is that they predict the Weibull-like empirical relationship between stomatal conductance and leaf water potential shown in Fig. 1, under the CMH in case 4 (Fig. 2A). In particular, because $-\Theta'(\psi_L)$ increases as ψ_L decreases, the "shoulder" of the Weibull-like beta function is displaced to the right of the shoulder of the Weibull conductivity function. In other words, stomates are adapted to shut before severely damaging their xylem. A Weibull-like beta function is also predicted under the WUEH in case 8, because it is easy to show that $\beta_{case8}(\psi_L) = \sqrt{\frac{\beta_{case4}(\psi_L)^2}{\lambda\beta_{case4}(\psi_L)^2+1}}$, which implies that $\beta_{case8}(\psi_L)$ is a monotonically increasing function of $\beta_{case4}(\psi_L)$. However, the shoulder of the beta function in case 8 will be displaced significantly to the right of the shoulder of the conductivity function only if λ is sufficiently small and/or $-\Theta'(\psi_L)$ is sufficiently large (Fig. 2A). Again, these are the conditions under which the WUEH converges to the CMH. If the reverse is true—the conditions most similar to those in CF77's simple model (6)—then plants will tend to damage their xylem before shutting stomates.

The beta function also decreases monotonically with ψ_L decreases in cases 3 and 7, but will have the shoulder of a Weibull-

like function only if $-\Theta'(\psi_L)$ is a sufficiently concave-up function of $-\psi_L$ (Fig. 2A). Together, the results in Table 1 show that

v) A nonconstant cost function ($\Theta'(\psi_L) \neq 0$) is necessary for a Weibull-like $\beta(\psi_L)$.
vi) A concave-up cost function and a Weibull conductivity function are sufficient for the Weibull-like $\beta(\psi_L)$, which is widely documented by data. Under the CMH, this function will cause stomates to shut before xylem potentials fall to the steep part of the conductivity function. However, under the WUEH, the reverse is true if λ is sufficiently large relative to $-\Theta'(\psi_L)$.
vii) Variable xylem conductivity is not necessary for a Weibull-like $\beta(\psi_L)$. The function will have the shoulder of a Weibull function even if conductivity is constant, if $-\Theta'(\psi_L)$ sufficiently accelerates as ψ_L decreases.

Exploration of a Mechanistic Model

A large body of work has examined stomatal response to passive hydraulic mechanisms (69–74), which has shown that the passive mechanisms alone would cause stomates to open as ψ_L falls, termed the "wrong-way response" because it is the opposite of what is observed. The wrong-way response occurs because of the mechanical force of the many desiccating epidermal cells on the relatively few guard cells (*SI Appendix 2*). In *SI Appendix 2*, we fuse the physico-chemical models of Peak and Mott and coworkers (74–76) with the simple models for the active regulation of guard cell osmotic potential by Buckley and coworkers (30, 73, 77, 78). We confirm that the beta function in our model is likely to be entirely caused by active regulation of guard cell osmotic potential, because passive water flow would cause the opposite behavior. We also introduce what is perhaps the simplest model for the active regulation of guard cell osmotic potential that would produce a Weibull-like beta function.

Discussion

We show here that a simple CMH for stomatal behavior is both consistent with empirical equations of stomatal conductance and an evolutionary stable strategy when plants compete for a common pool of water. This CMH arises from consideration of the costs of low water potentials to the plant, which are numerous and widely documented. We further introduce the concept of the marginal xylem tension efficiency—how much carbon a competitively optimal plant is willing to forego from opening its stomates marginally more to avoid a drop in water potential (increase in xylem tension)—which is useful because it allows clear discrimination and testing of the CMH and WUEH optimizations (Fig. 2).

The WUEH and CMH optimizations represent different points on the spectrum of plant competition for water. Under the WUEH, an individual plant should reduce its carbon gain by reducing its stomatal aperture whenever a change in edaphic conditions increases the rate of evaporation. However, because plants compete episodically for water and have overlapping root systems, this makes sense only if the plant's neighbors "voluntarily" do the same for the good of them all, rather than gain a competitive edge by taking the water that the plant has voluntarily left in the soil (47). For this reason, regulating stomata to maintain constant marginal water use efficiency is an example of a cooperative game theoretic equilibrium. The cooperative strategy will maximize ecosystem-level productivity, but makes sense for an individual plant only if its neighbors cooperate. In contrast, the pure carbon maximization approach developed here is an example of a competitive or Nash equilibrium, because maximizing carbon gain under all edaphic conditions is the winning strategy when neighbors are pure competitors, even though selfish water use that maximizes carbon gain reduces ecosystem-level productivity.

We find, however, that the CMH optimization reproduces all of the same empirical relationships as the WUEH optimization (e.g., Eq. **15**) and thus is, at the very least, a potential alternative to WUEH that has a strong ecological rationale under competition for water. We observe that these two optimizations look largely similar during wet conditions but imply different stomatal behavior during drought conditions. We emphasize that this divergence should manifest at all time scales, occurring even at daily time scales [e.g., varying vapor pressure deficit (VPD) with relatively constant soil water potential] where WUEH suggests λ should be constant. Thus, if λ is observed to vary substantially at daily time scales with conditions that might affect hydraulic costs (e.g., varying VPD), this would be a useful test of the WUEH optimization. For example, multiple studies have observed some variation in λ at diurnal time scales (17, 21, 22, 24, 79).

At longer time scales where soil moisture varies substantially, much research has highlighted that λ should change over weekly, seasonal, and interannual scales dependent on drivers such as phenology and soil water potential (11, 12, 28, 32, 33, 40, 43, 80). Indeed, empirical studies of changes in λ associated with long-time-scale changes in ψ_L have revealed a wide diversity of patterns, including increasing, decreasing, and humped relationships (11, 15, 24, 81). However, after accounting for cuticular conductance, which most studies ignore, ref. 11 observed that data from a variety of species are consistent with the hypothesis that λ increases exponentially as ψ_L falls. We find in Eq. **13** that the pure carbon-maximization optimization predicts that λ should be a steeply concave-up function of falling ψ_L at all time scales, although larger seasonal and interannual variation in soil water potential would be most likely to reveal the shape of this function.

We show in cases 1–8 (Table 1) that including the carbon costs of low water potential is critical to reproducing a Weibull-like down-regulation of stomatal conductance and that this down-regulation is most realistic with variable xylem conductivity (cases 4 and 8 in Fig. 2*A* vs. figure 1b in ref. 82). Again, decades of literature have shown that xylem conductivity varies in response to leaf water potential (49). Although the the $\beta(\psi_{leaf})$ functions predicted in cases 4 and 8 are qualitatively similar, in that they are both Weibull-like (Fig. 2*A*), the CMH (case 4) will generally shut stomata at higher water potentials than the WUEH (case 8), all else being equal, which could have significant hydrologic consequences during drought. The large differences between the MXTE functions predicted by the WUEH and the CMH offer perhaps the best way to discriminate between the two (Fig. 2*B*).

It should be possible to probe the relative contributions of the CMH and the WUEH in stomatal behavior from observational data, revealing the optimization that stomata perform in different settings. Testing stomatal optimizations has been remarkably challenging because the topologies of $\partial A/\partial g_s$ and $\partial E/\partial g_s$ are sensitive to many variables (30, 83). Our results reveal an avenue to test the optimization stomata perform would be to estimate both λ and $\Theta'(\psi_L)$ from data. Imagine that we close the system (Eqs. **3–8**) with a seventh equation of the form $z(\psi_L) = $ MXTE from case 8 in Table 1,

$$\lambda K(\psi_L) + (I + S\psi_L) = \frac{\frac{\partial A_N}{\partial g_s}}{-\frac{\partial E}{\partial g_s}}, \qquad \textbf{[17]}$$

where I and S are constants and $(I + S\psi_L) = -\Theta'(\psi_L)$. Together, **[3–8]** and **[17]** predict C_i, C_{gain}, T_L, A_N, E, ψ_L, and g_s from the seven edaphic inputs in $\mathbf{I_E}$, if the values of all of the constants including S and I are known. Now suppose that one has a dataset containing measured values of some subset of C_i, T_L, A_N, E, ψ_L, and g_s for a range of values of $\mathbf{I_E}$. If one first chooses values for λ, S, and I and the other constants, one can then calculate the

difference between each observed value of C_i, T_L, A_N, E, ψ_L, or g_s and the value predicted by the model of Eqs. **3–8** and **17**. By inverting this process, one could estimate the values of λ, I, and S that provide the best match between predicted and observed. A concave-up cost function is indicated by significantly positive (as opposed to zero) $((I + S\psi_L) > 0)$ with significantly negative slope (estimated $S < 0$). The CMH model is supported by parsimony if λ is not significantly different from zero, because the MXTE in case 8 becomes the MXTE in case 4 if $\lambda = 0$. This analysis would provide the most rigorous test of the WUEH relative to the CMH if data were restricted to short periods, such as a single day. The relative magnitudes of the two estimated terms in the MXTE would quantify the relative importance of hydraulic costs and water shadow pricing (λ) and allow direct estimation of the functional form of the MXTE (Fig. 2*B*). We note, however, that inversion analyses using **[3–8]** and **[17]** should be restricted to plants in which all leaves are expected to have similar xylem potentials and similar edaphic inputs (i.e., plants in full sun without a lot of self-shading). Otherwise, Eqs. **6** and **7** would have to account for variation among leaves. A model of a plant like **[3–8]**, but with a realistic branching structure and data-constrained estimates of the segmentation of hydraulic resistances, might allow one to invert a wide variety of data including data from eddy covariance towers. Another promising avenue of future research could be exploring the interlinked hydraulic–stomatal–photosynthesis model in light of the direct temperature sensitivity of the photosynthesis and conductivity equations.

Other stomatal models driven by leaf or soil water potentials have been proposed and incorporated into ecosystem models (73, 78, 84, 85). These models often replace the VPD dependence entirely with a sensitivity to water potential. Indeed, these models appear to perform with comparable accuracy to other empirical models where they have been tested (84, 85), although more thorough tests across a wide array of species, biomes, and water use strategies are needed. These models are useful steps to better integrate water relations with stomatal behavior and our work provides a unifying, parsimonious theoretical background. Whereas water potential-driven stomatal models might appear on the surface to struggle with capturing isohydric behavior—where stomatal conductance falls rapidly to maintain diurnal water potentials relatively constant—Buckley (30) describes how this homeostatic feedback behavior can nonetheless emerge from hydraulic regulation of the stomatal aperture where relatively few cells compose the humidity sensor and are separated but not isolated from the bulk of leaf water by a large resistance.

At larger scales, most stomatal algorithms in ecosystem models to date operate in the "big leaf" paradigm, with minimal physiological connection between the leaf and plant water status. However, the ubiquity of a phenomenological function in most Earth system models that suppresses stomatal conductance as soil water reserves fall (35, 86–88) underscores that current leaf-level models alone are not sufficient for simulating stomatal responses in land surface models. More physiologically based stomatal algorithms have strong potential to improve simulation of carbon, water, and energy fluxes in models and increase confidence in predicting vegetation response to climate extremes.

Note. *Supporting Information* contains a description and extended derivation of the stomatal conductance model.

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