A Model Predicting Stomatal Conductance and its Contribution to the Control of Photosynthesis Under Different Environmental Conditions.

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In the past, stomatal responses have generally been considered in relation to single environmental variables in part because the interactions between factors have appeared difficult to quantify in a simple way. A linear correlation between stomatal conductance (g) and CO_2 assimilation rate (A) has been reported when photon fluence was varied and when the photosynthetic capacity of leaves was altered by growth conditions, provided CO_2, air humidity and leaf temperature were constant (1). Temperature and humidity are, however, not consistent in nature. Lack of a concise description of stomatal responses to combinations of environmental factors has limited attempts to integrate these responses into quantitative models of leaf energy balance, photosynthesis, and transpiration. Moreover, this lack has hindered progress toward understanding the stomatal mechanism. We have taken a multi-variant approach to the study of stomatal conductance and we show that under many conditions the responses of stomata can be described by a set of linear relationships. This model can be linked to models of leaf carbon metabolism and the environment to predict fluxes of CO_2, H_2O and energy. In this paper, we show how the model of conductance can be linked to a description of CO_2 assimilation as a function of intercellular CO_2 (whether empirical or the output of a model) to predict the distribution of flux control between the stomata and leaf "biochemistry" under conditions in a gas-exchange cuvette.

Methods

CO_2 assimilation (A) and conductance (g) were measured as we varied conditions over the following wide range: photosynthetically active photon fluence (I) from 0.1 to 2.0 mmol m^{-2} s^{-1} the concentration (mole fraction) of CO_2 at the leaf surface (c_s) from 100 to 1000 μmol mol^{-1}, temperature (T) from 20 to 35°C, and the diffusion gradient for water vapor between the intercellular air spaces and the leaf surface (w_s) from 2 to 30 mmol mol^{-1}. We express gas concentrations external to the leaf in terms of mole fraction at the leaf surface (interior to the boundary layer) so that the results apply to any boundary layer conditions.

Results

A linear relationship between A and g when I was varied is apparent in our data but when other factors are varied the relationship of g to A is less straight forward (Fig. 1a). Several patterns are, however, present when CO_2 or humidity are varied while all other factors are held constant.

Stomatal conductance tends to decline with increasing CO_2 concentration while assimilation increases. It has been shown that the intercellular mole fraction CO_2 (c_i) changes linearly with ambient mole fraction CO_2 (1). When air humidity is decreased stomata tend to close while relatively little change in assimilation rate occurs. Humidity responses at different values of I through which A and g vary widely converge toward a single relationship where the ratio A/g is a linear function of humidity (2).

The data of Fig. 1a may be replotted showing stomatal conductance to water vapor (g_{sw}) varies directly with assimilation rate (A) scaled by relative humidity at the leaf surface (h_s), and divided by the mole fraction CO_2 at the leaf surface (c_s). This is a simple empirical model of stomatal conductance which can be expressed as

$$g_{sw} = kA\frac{h_s}{c_s} \qquad (1)$$

This model accounts for variations in stomatal conductance when, as in nature, several environmental factors are changing at once. The slope constant of the model (k) represents the
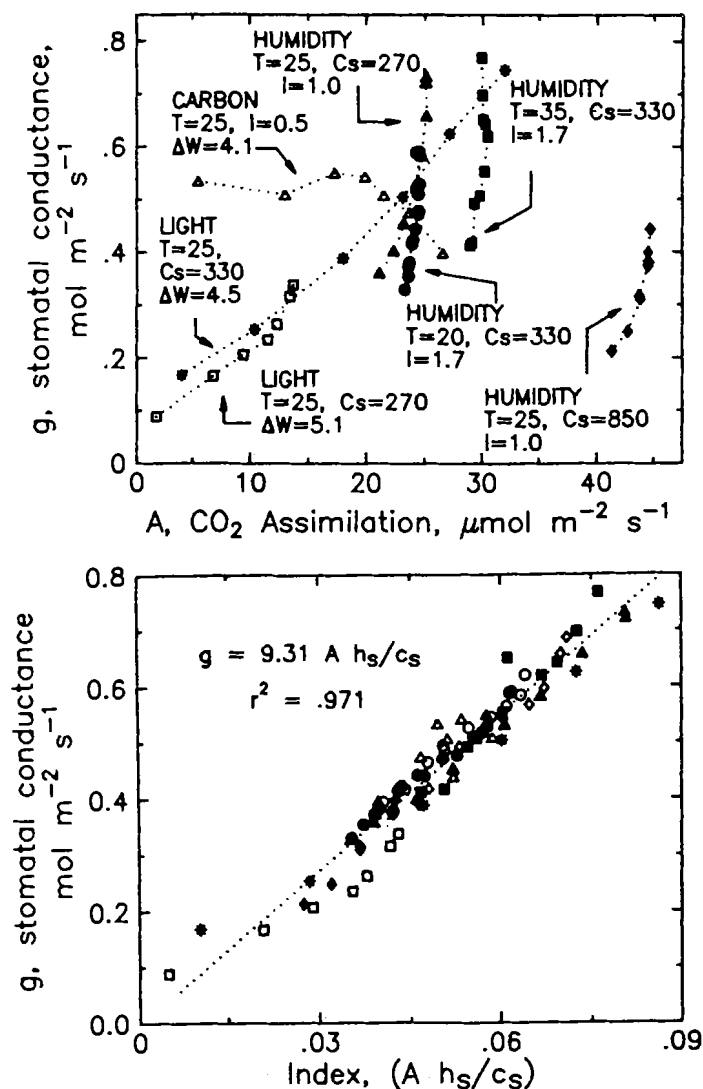
Figure 1. (A) Patterns in the relationship of g to A as humidity, light, and CO_2 concentration were changed under different environmental conditions as labeled in the figure.

(B) A simple empirical model of stomatal conductance in *Glycine max*. The linear relationship of conductance to a combined environmental-physiological index: the product, net CO_2 assimilation times relative humidity at the leaf surface divided by the CO_2 concentration at the leaf surface. The model (dotted line) is an unconstrained regression (intercept not significantly different from the original) of the data shown here. A = net CO_2 assimilation rate (μmol m^{-2} s^{-1}), h_s = decimal relative humidity (w_s/w_i, unitless) and c_s is mole fraction times 10^6 (μmol mol^{-1}). The data are those in Figure 1a (represented by the same symbols).

composite sensitivity of stomatal conductance to assimilation, CO_2 concentration, humidity and temperature. The intercept of the regression through the data of Fig. 1 is not significantly different from the origin. Regression lines through data from other species have different slopes and some have slightly positive y-intercepts (Ball and Berry unpublished).

Of particular interest is the interaction of temperature, humidity and the assimilation rate in controlling conductance. The stomatal response to humidity has been presumed to be a function of the driving force of transpiration (ΔW), the gradient of water vapor concentration between the leaf and the air (4). Varying humidity while the leaf is held at different temperatures shows g_{sw} is less sensitive to ΔW at higher temperatures (Fig. 2a). The change in sensitivity may relate to the large change in saturation mole fraction water vapor (w_{sat}) with temperature. Relative humidity at the leaf surface (h_s) scales w_s for changes in w_{sat}. ($h_s = 1 - w_s/w_{sat}$). Scaled both by w_{sat} and by A, the response of stomatal conductance to humidity converges to a single relationship (Fig. 2b). From this we conclude that stomata respond to relative humidity. The response of g_{sw} to temperature include responses to relative humidity and to assimilation rate.

There are a number of ways that this model of stomatal behavior can be used including simulation of leaf responses in nature. We describe below a less obvious use of the model, namely how it can be used to estimate stomatal "limitation" of photosynthesis.

Discussion: Application of the empirical model to the calculation of the control of CO_2 flux.

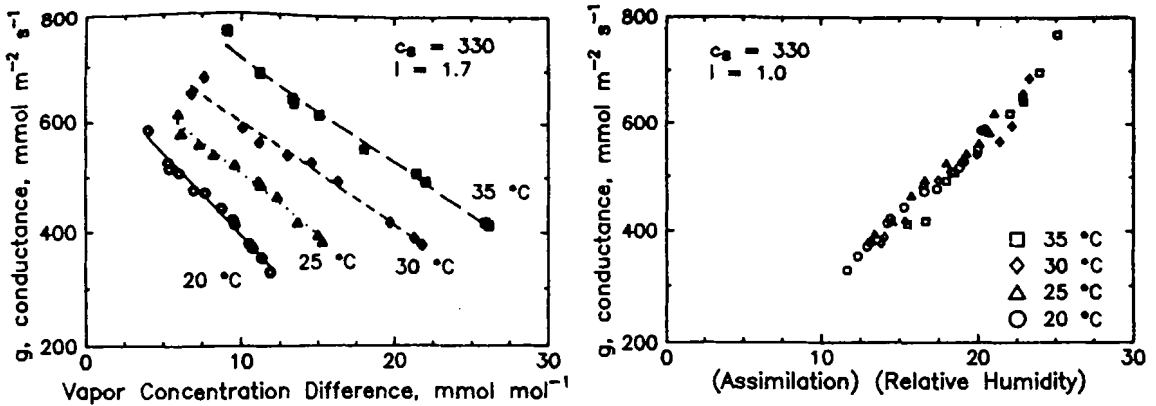A number of expressions for the stomatal limitation of photosynthesis have been suggested (4)

Figure 2. The interacting effects of temperature and humidity on stomatal conductance. I was 1.7 mmol m^{-2} s^{-1} and c_s was 330 μmol m^{-2} s^{-1}.
(A) Stomatal conductance as a function of vapor concentration difference at temperatures ranging from 20 to 35°C.
(B) Stomatal conductance as a function of net CO_2 assimilation rate times relative humidity of the sub-boundary-layer air (w_s/w_i) at 20, 25, 30, and 35 degrees (°)

but these generally fail to adequately consider non-linearities of the photosynthetic system and/or would attribute possible feedback from non-stomatal components of the system (e.g. leaf biochemistry) to stomata. The analysis of metabolic control outlined by Kacser and Burns (5) is ideally suited to quantitative descriptions of the control of fluxes in complex systems.

Control analysis defines the control coefficient of system component P with respect to flux V as

$$C_P^V = \frac{\partial V \cdot P}{\partial P \cdot V} = \frac{\partial \ln V}{\partial \ln P} \qquad (2)$$

In the present case we consider the flux of CO_2, A, through a two system: the stomatal (s) and the "biochemistry" (c). Since the sum of all control coefficients in a system is unity the control coefficient for one component can be thought of as roughly the proportion of total "limitation" at that step (5). The "biochemistry" component here is comprised of all aspects of carbon metabolism downstream of c_i.

The expression for the control of stomata with respect to CO_2 assimilation, derived in (6) becomes

$$C_S^A = \left[1 - \frac{(c_s - c_i)g' - g_{sc} - \frac{E}{2}}{A'}\right]^{-1} \qquad (3)$$

(where g_{sc} is stomatal conductance to CO_2, E is transpiration rate, g and A' are the slopes of g_{sc} and A as function of c_i, respectively) when leaf temperature is held constant, boundary layer conductance is large and known, and w_s and c_s calculable, --typical conditions for many gas exchange experiments.

If one ignores the influence of the efflux of water from a leaf on the diffusion of CO_2 into the leaf using the approximation $A = g_{sc}[c_s-c_i]$ and substitutes for A in Eq. 1 the empirical model of conductance can be rearranged to

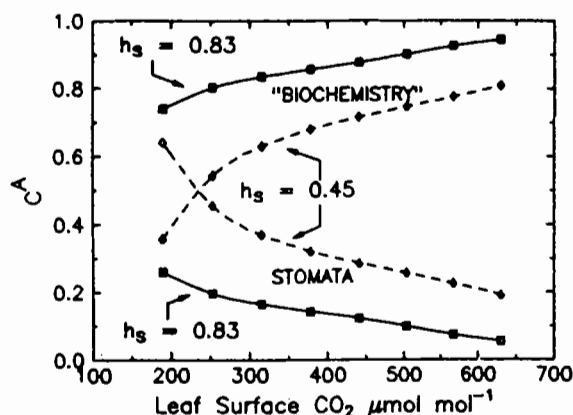$$\frac{c_i}{c_s} = 1 - \frac{1.6}{h_s k} \qquad (4)$$

Figure 3. The distribution of control of CO_2 assimilation between the "biochemistry" and the stomata as a function of the mole fraction CO_2 at the leaf surface. The relative humidities of the air at the leaf-surface was 0.83 (solid lines) and 0.45 (dashed lines) at leaf temperature of 25°C.

Obtaining an expression for g' from the empirical model and substituting into Equation 3

$$C_S^A = A'\left[\frac{kAh_s}{c_s(h_s k - 1.6)} + \frac{kAh_s}{1.6c_s} + \frac{E}{2}\right]^{-1} \tag{5}$$

This equation is parameterized with the slope of an empirical relationship as in Fig. 1b, measured or modeled values of A and A' and external conditions h_s and c_s. A more complete analysis of stomatal control, applicable in nature, that considers control of evaporation, convective heat transfer, radiative exchange, as well as CO_2 fixation and that includes control due to the boundary layer as well as stomata and "biochemistry" is available (6).

The distribution of flux control with changes in mole fraction CO_2 at the leaf surface at two humidities (Fig. 3) illustrates the interaction of two environmental variables in the "limitation" of photosynthesis. At low external CO_2 concentrations diffusion of CO_2 through stomata constitutes a large portion of the control but as CO_2 concentration increases the "biochemistry" tends toward saturation clearly dominating the rate of CO_2 fixation. At low humidity stomata can constitute the major control of assimilation and can retain significant control to higher CO_2 concentrations. This rise in stomatal control of A is accompanied by a reduction in A (Fig. 1) and reflects a "cost" in terms of carbon gain attached to the "benefit" of reducing water loss.

Conclusion

The empirical model of stomatal conductance presented here provides new fundamental insight into the nature and interaction of stomatal responses particularly with regard to humidity. We have suggested several ways that the model can be used including the calculation of the control coefficients of stomata and biochemistry with regard to assimilation. This approach to quantifying "limitation" has several advantages including: expandability to include additional system components (e.g. boundary-layer, or more specific aspects of the "biochemistry") and ability to illustrate interactions between and the distribution of control among all components of an integrated system (6).

Acknowledgments

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