Establishing the relationship between stomatal conductance and microclimate through a model of stomatal conductance

Jinzhi Wang

Introduction

I came to CGREC on May 7, 2008 to work under the direction of Dr. Xuejun Dong, eco-physiologist at the Center. His work involves the relationship between environmental factors (precipitation, temperature, and radiation) and soil respiration and plant physiology (leaf photosynthetic rates and leaf area index) of dominant species. One of the key objectives is to calculate canopy photosynthesis based on field-measured physiological data.

Stomata are tiny pores on the underside of a plant leaf that allow for gas exchange. The pores are formed by a pairs of guard cells that are responsible for regulating the size of the opening. Carbon dioxide (CO_2) enters the plant through these openings where it is used in photosynthesis and respiration. Also, water vapor is released simultaneously into the atmosphere through these pores in a process called transpiration. Therefore, a reliable model of stomatal conductance is useful in ecosystem simulation and analysis involving both photosynthesis and transpiration (Raich *et al.* 1991; Gao *et al.* 2002).

Stomatal conductance has been experimentally shown to be related to net CO_2 assimilation rate, environmental vapor pressure deficit, soil water stress, and intercellular CO_2 concentration, etc. A number of empirical and mechanical stomatal conductance models have been developed based on these experimental and observational studies (Jarvis 1976; Ball *et al.* 1987; Gao *et al.* 2002; Buckley *et al.* 2003). The multiplicative stomatal model by Jarvis (1976) can be useful under certain conditions, but might have limited capability when used under a different situation due to the lack of biologically-based mechanisms included in the model. The model by Buckley *et al.* (2003), on the other hand, might be quite universal relating stomatal conductance to various sub-cellular processes, but it is expensive for a full calibration. In field ecophysiological studies, however, we need a model that has some mechanistic considerations built in it, but is easy to calibrate with routinely available data. Models by Ball *et al.* (1987), Gao *et al.*(2002) and Gao *et al.* (2005) fall into this category. However, the Gao *et al.*(2002) model seems to be the simplest, because it only requires soil water potential, relative vapor pressure deficit, and photosynthetically active radiation values. This semi-mechanistic model, with its clear biophysical mechanisms, has a potential for applications to different ecosystems. The objective of our present study was to test this new stomatal model by Gao *et al.*(2002) for use in a mixed-grass prairie in the United States.

Methods

The model description

A four-parameter stomatal conductance model, as developed by Gao *et al.* (2002), relates stomatal conductance (g_s; mmol m^{-2} s^{-1}) to soil water potential (ψ_s; kPa), photosynthetically active radiation (I_p; μmol m^{-2} s^{-1}) and relative vapor pressure deficit (d_{vp}; calculated as absolute vapor pressure deficit (VPD) divided by air pressure p_a):

$$g_s = \frac{g_{0m} + k_\psi \psi_s + k_{\alpha\beta} I_p}{1 + k_{\beta g} d_{vp}} \qquad (1)$$

where g_{om} (mmol m^{-2} s^{-1}) is the maximum possible stomatal conductance at dark with zero soil water potential (at saturated soil water content), k_ψ (mmol m^{-2} s^{-1} kPa^{-1}) is the elastic compliance of guard cell structure defined as the decrease in g_s induced by a 1 kPa decrease in ψ_s, and hence is indicative of the drought resistance capability of plant species, $k_{\alpha\beta}$ (mmol μmol^{-1}) is the sensitivity of g_s to I_p and is related to the sensitivity of guard cell osmotic potential to photosynthetic radiation and the elastic compliance of guard cell structure, and $k_{\beta g}$ (dimensionless) describes the dependence of g_s on VPD.

Site description

The study was conducted at the Central Grasslands Research Extension Center, 7.5 miles northwest of Streeter in south-central ND, lat 46º46′ N, long 99º28′ W. The study site is typical of rangeland in the Missouri Coteau. The elevation of the study site is about 1926 ft. This area has a continental climate, with an average January temperature of 3.2 °F and an average August temperature of 68 °F. On average, there are 131 frost-free days per year. Mean annual precipitation is 17.87 in., with about 72% of the precipitation occurring during the growing months from May to September. Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), western wheatgrass (*Pascopyrum smithii*), white sage (*Artemisia ludoviciana*), and western snowberry (*Symphoricarpos occidentalis*) are among the dominant species (Patton *et al.* 2007).

Data collection and model parameterization

During the 2008 growing season, we measured photosynthetic rates of dominant range plants using a LI-6400 Portable Photosynthesis System with the standard leaf chamber and a 6400-01B LED light source). These measurements were made on plants in both a moderately and a heavily grazed pasture. In each pasture, the measurements were made both outside and inside of a rain-out shelter receiving 70 %

of long-term average precipitation. All measurements were made on mostly clear days from 9:00 am to 12:30 pm. Both the water and CO_2 scrubbers were adjusted to full bypass so that the humidity and CO_2 concentration of the incoming air was minimally changed from the ambient values. The internal light level was adjusted according to that of an external light sensor attached to the equipment. Eventually, however, the external light level was used in calibrating the Gao *et al.* (2002) model. All measurements were made within 5-7 minutes to insure that the measured stomatal conductance was unchanged from the equilibrated level immediately prior to the measurement. Only sunlit leaves were used in the measurements. Stomatal conductance, photosynthetically active radiation, relative humility (Rh), and air temperature and pressure were also recorded by the equipment every week. We also used a neutron moisture probe to measure soil water weekly.

Relative vapor pressure deficit was calculated as:

$$d_{vp}= (e^* - e^* \text{ x } \mathrm{Rh})/ \mathrm{P_a} \qquad (2)$$

where e^* was obtained using the Goff-Gratch (1946) equation:

$$\begin{aligned}\log e^* &= -7.90298(T_{st}/T-1)+5.02808\log(T_{st}/T)-1.3816\times10^{-7}(10^{11.344(1-T/T_{st})}-1)\\ &+8.1328\times10^{-3}(10^{-3.49149(T_{st}/T-1)}-1)+\log e^*_{st}\end{aligned} \qquad (3)$$

in which log refers to the logarithm in base 10, e^* is the saturation water vapor pressure (hPa), T is the absolute air temperature in degrees Kelvin, T_{st} is the steam-point temperature (373.15° K), and e^*_{st} is e^* at the steam-point pressure (1013.25 hPa).

Soil water potential (ψ_s) was calculated according to Campbell (1974):

$$\psi_s = \psi_{\max}(\theta_{\max}/\theta)^q \qquad (4)$$

Where ψ_s is soil water potential; θ is soil water content; $\psi_{\max}$ is the maximum soil water potential when soil is fully saturated with water ($\theta_{\max}$); q is an empirical parameter. Values for $\psi_{\max}$, $\theta_{\max}$, and q were determined by Dong *et al.* (2001)).

Soil water potential for different soil depths was calculated from measured soil water content values and weighted according to typical root vertical distribution (Dahlman & Kucera 1965) to find the average soil water potential, which was used in the model.

Results and Discussion

The results and all parameters of the non-linear regression estimation from the field photosynthesis measurements of the seven dominant species are shown in Table 1. For each species, measurements from the pastures of heavy and moderate grazing were pooled as a first try. Graphs in Figure 1 plot the model predicted stomatal conductance against those observed in the field for the dominant species. The calculated values of stomatal conductance fit the measured ones quite well for *Stipa viridula*, *Poa pratensis*, and *Symphoricarpos occidentalis*. However, calculated values were not close to the measured values for the other species. We also predicted the stomatal conductance of species in the drought environments (Figure 2). Even though the results are not consistent as those predicted in studies by Gao *et al.* (2002; 2003) and Liu *et al.* (2006), there are several factors that probably affected the results. The poorly fitting values were partly due to the less satisfactory calibration using the pooled data. It is also possible that the plants growing under the drought treatments might undergo different trajectories in stomatal conductance, compared with those from the natural conditions. Also, we conducted our research in a grassland instead of a forest ecosystem, where the Gao *et al.* (2002) model was developed.

However, considering the simplicity of this model and other assumptions and peculiarities we used in carrying out the field measurements (for example, leaves of all of our species are small, which can influence the measurements' precision), the model's behavior as shown in Figures 1 and 2 is still quite positive.

Also, if we separately calibrate the Gao *et al.* (2002) model for the grazing treatments, we will get much better results for dominant species (See Table 2 and Figure 3). These results suggest that the Gao model (2002) is promising for use on species in the mixed-grass prairie. Also, it appears that separately treating plants from different grazing intensities is necessary in order to better calibrate the model. We hope to collect more field data next year to get more satisfactory results.

Table 1. Estimated parameters for the dominant species using the stomatal conductance model

Species	g_{om}	$k_{\alpha\beta}$	$k_{\beta g}$	k_{ψ}	S	R^2
Bromus inermis	44.07	0.01	0.16	-14.02	0.5076	0.247
Poa pratensis	285.40	0.05	0.08	26.29	0.4199	0.306
Stipa viridula	153.30	-0.03	0.04	-17.90	0.8411	0.810
Symphoricarpos occidentalis	21.41	0.04	0.27	15.22	0.5750	0.376
Solidago rigida	389.60	0.06	-0.04	-16.55	1.2367	0.359
Artemisia ludoviciana	423.00	0.12	0.57	115.4	0.5847	0.235
Cirsium flodmanii	1409000	1521	1789	555800	0.4216	0.307

S is an index to measure how well the predicted values of the dependent variable fit those observed values, $S = \left[\sum_{i}^{n} \frac{|O_i - P_i|}{O_i} \right] / n$, O_i, P_i and i are the observed and predicted values of the dependent variable, and sampling size, respectively.

Table 2. Estimated parameters for the dominant species using the stomatal conductance model

Grazing treatment	Species	g_{om}	$k_{\alpha\beta}$	$k_{\beta g}$	k_{ψ}	S	R^2
Moderate Grazing	*Bromus inermis*	69.49	0.22	-12.05	0.04	0.4537	0.513
	Poa pratensis	285.25	0.08	27.45	0.03	0.4326	0.182
	Symphoricarpos occidentalis	434.47	-0.07	-0.77	0.03	0.4978	0.186
	Solidago rigida	394.94	-0.11	-18.10	0.03	0.2972	0.608
Heavy grazing	*Bromus inermis*	279.29	0.08	5.96	-0.142	0.4418	0.082
	Poa pratensis	169.61	0.20	20.92	0.04	0.2521	0.377
	Stipa viridula	235.32	0.11	2.73	0.04	0.3811	0.154
	Artemisia ludoviciana	200.47	-0.08	-24.80	0.01	0.1674	0.855
	Symphoricarpos occidentalis	124.74	0.22	19.62	0.12	0.3387	0.355

S is an index to measure how well the predicted values of the dependent variable fit those observed values, $S = \left[\sum_{i}^{n} \frac{|O_i - P_i|}{O_i}\right]/n$, O_i, P_i and i are the observed and predicted values of the dependent variable, and sampling size, respectively.

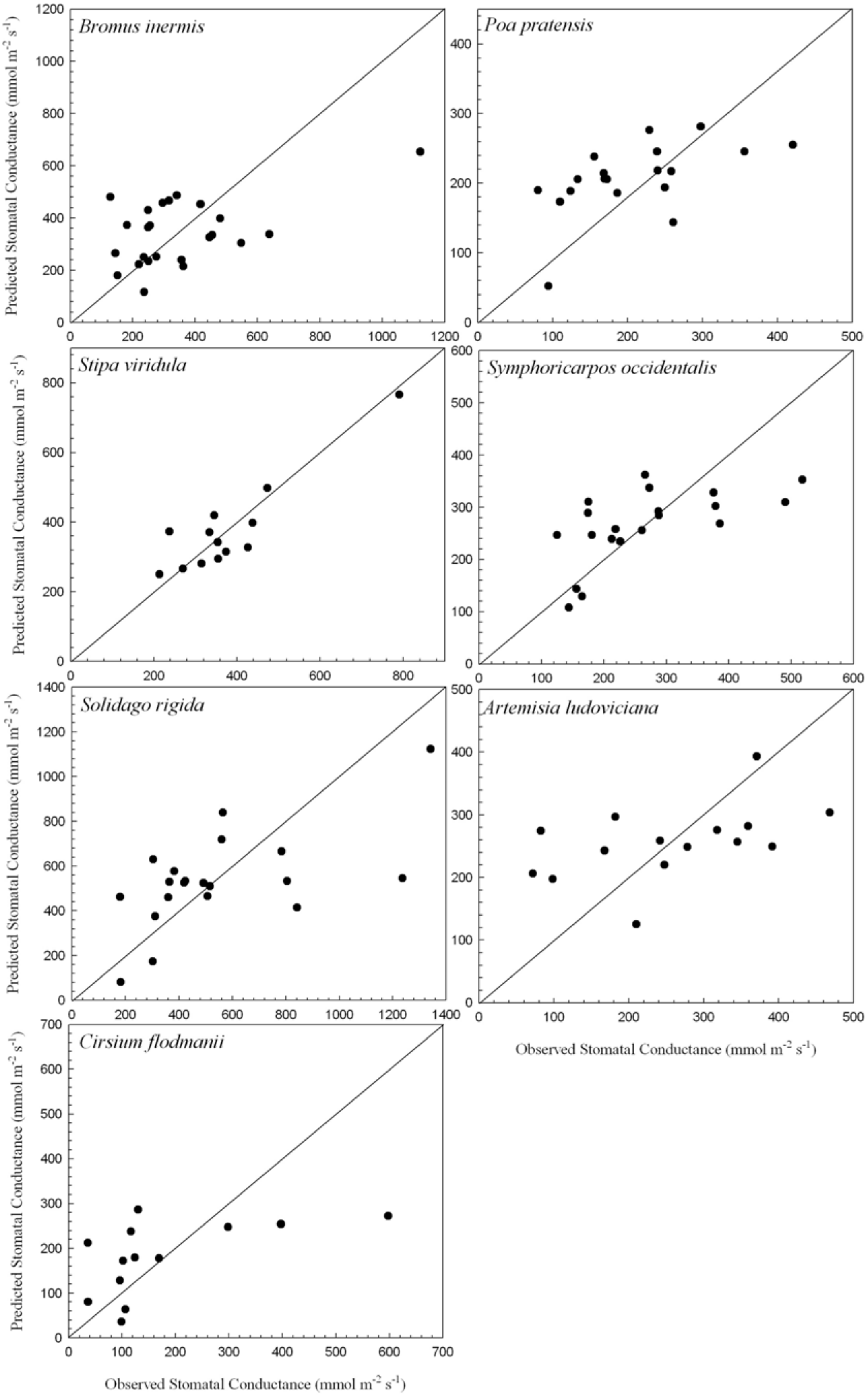

Figure 1. Application of the stomatal conductance model to the dominant species in mixed-grassland at CGREC in 2008.ND

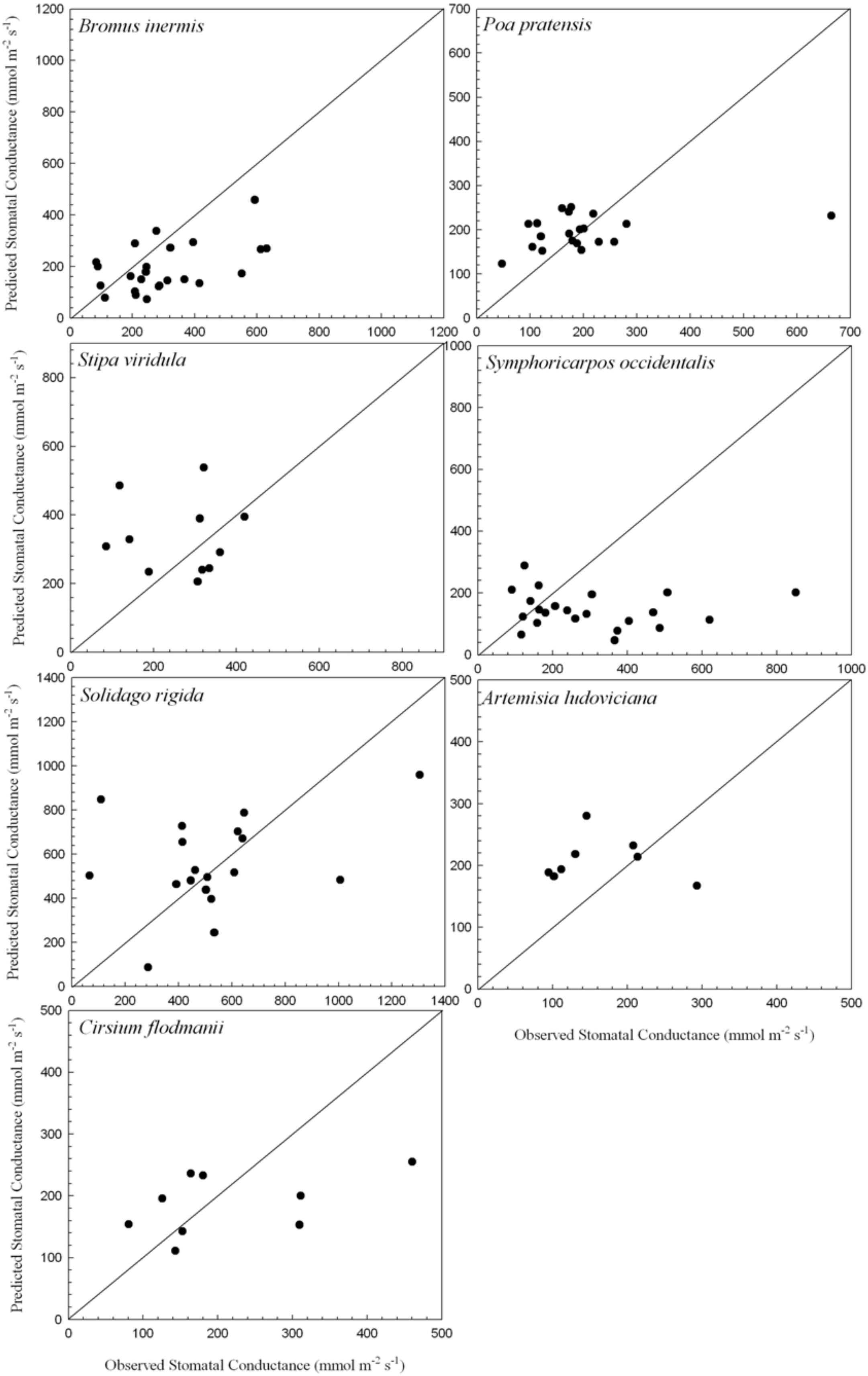

Figure 2. Application of the stomatal conductance model to the dominant species in the drought environment in mixed-grassland at CGREC in 2008.

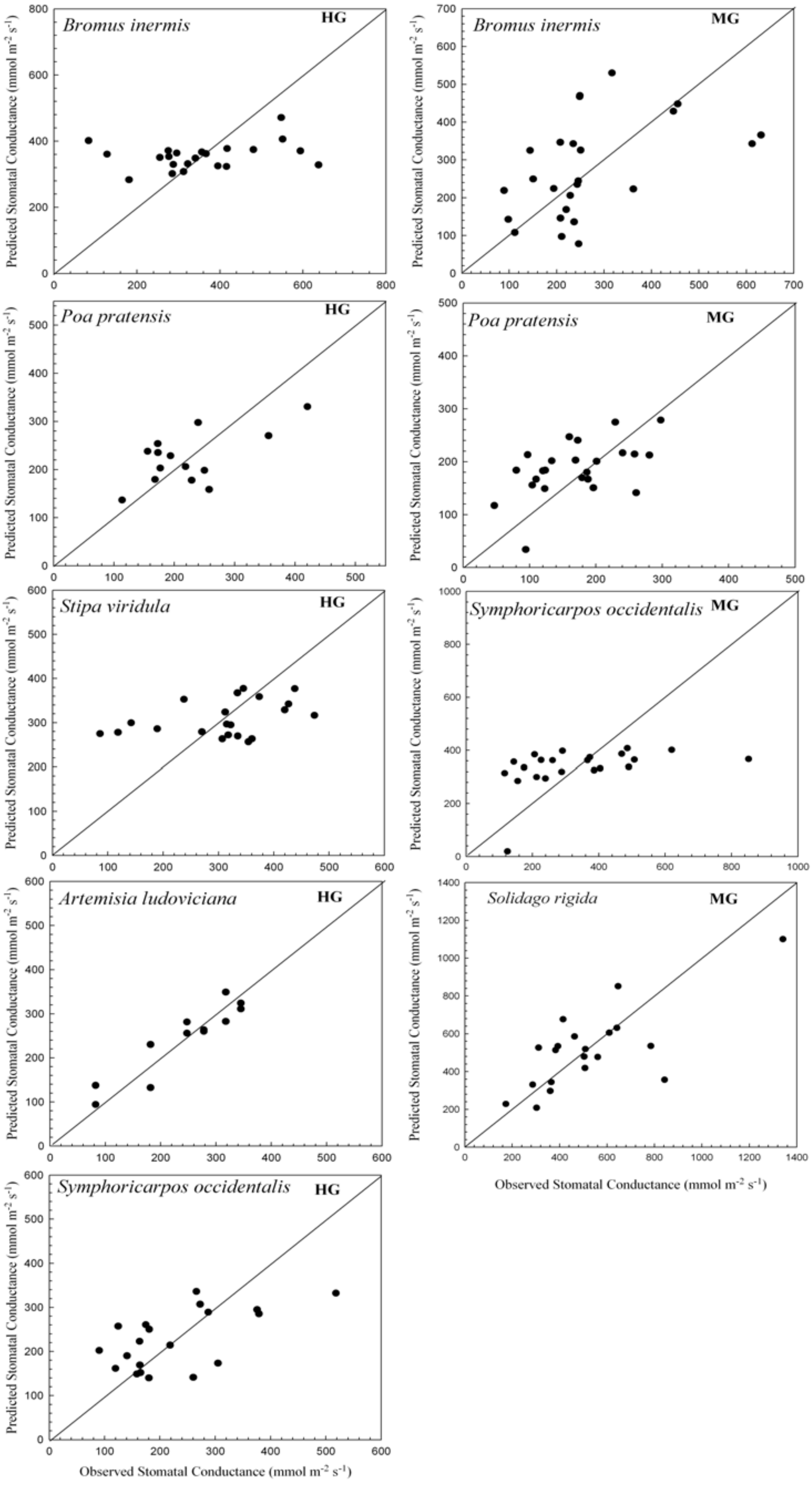

Figure 3. Application of the stomatal conductance model to some of the dominant species in mixed-grassland under heavy grazing (HG) and moderate grazing (MG) at CGREC in 2008.

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