

半干旱地区 3 种植物叶片水平的抗旱耐旱特性分析 ——两个气孔导度模型的应用和比较

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摘要 在对半干旱区 3 种植物进行生理生态特性测定的基础上, 应用两种气孔导度模型进行参数的非线性拟合, BBL 模型平均可以解释 77.6% 的结果, Gao 模型平均可以解释 59.3% 的结果。但 Gao 模型作为一个机理性的模型, 其参数具有明确的物理意义。模型的行为和敏感性分析结果说明, 用 BBL 计算的气孔导度一般大于 Gao 模型。BBL 模型对于干旱胁迫下的土壤水分亏缺没有响应, 因而不适合用作干旱半干旱区的植物生理生态学分析和生态系统模拟。而 Gao 模型可以描述在各种水分条件下植物气孔导度的响应。Gao 模型的结果说明, 与油松 (*Pinus tabulaeformis*) 和中间锦鸡儿 (*Caragana intermedia*) 比较, 小叶杨 (*Populus simonii*) 具有最小的抗旱和耐旱能力, 油松具有最好的叶片水平的耐旱和抗旱特性, 但其气孔导度对土壤水分的不敏感意味着在干旱条件下维持光合作用的同时, 也可能导致过多的水分损失。中间锦鸡儿具有很强的耐旱性, 且其气孔导度对土壤水分的变化敏感, 二者相结合, 中间锦鸡儿可以在土壤水分条件较好的情况下, 维持较大的气孔导度以满足光合作用的需要, 但在土壤水分胁迫严重的时候能迅速降低气孔导度以保持土壤水分。

关键词 气孔导度 抗旱性 敏感性分析 气孔模型

LEAF-SCALE DROUGHT RESISTANCE AND TOLERANCE OF THREE PLANT SPECIES IN A SEMI-ARID ENVIRONMENT: APPLICATION AND COMPARISON OF TWO STOMATAL CONDUCTANCE MODELS

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Abstract We measured diurnal gas exchange properties of three major species in a semi-arid site, and two stomatal conductance models were then applied to the data. The result indicated that the BBL model and the Gao model could explain on average 77.6% and 59.3% of variation in the observed stomatal conductance, respectively. Sensitivity analysis of the models indicated that the BBL model tended to give higher predictions of stomatal conductance than the Gao model. Both models showed similar responses to changes in vapor pressure. The sharp contrast between the two models, however, was that the Gao model responded to changes in soil water stress to different extents. The BBL model coupled with the T_J photosynthesis model was indifferent to increases of soil water stresses, which contradicts concurrent understanding and observations about plant physiology in arid and semiarid regions. Thus the BBL model, even though it provided better explanations of the variations in field stomata data, may not be appropriate for experimental data analysis and ecosystem simulation applications. The analysis using the Gao model indicated that *Populus simonii* was the least tolerant and resistant to water stresses among the three species studied. *Pinus tabulaeformis* had both high tolerance and resistance, but stomatal conductance of the pine tree was the least insensitive to changes in soil water stresses. Hence this pine tree may not be good for water conservation under extremely dry conditions. *Caragana intermedia*, however, had both larger drought tolerance and larger sensitivity to incremental soil water stresses, and thus can provide large stomatal conductance for photosynthesis when soil water stress was low, but reduce water consumption under severe water stresses by decreasing stomatal conductance with increasing soil water stress.

Key words Stomatal conductance, Drought resistance, Sensitive analysis, Stomatal model

Gas exchange of plants in arid and semi-arid regions was strongly controlled by stomatal conductance in various

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lab and field experiments (Dong & Zhang, 2001; Li *et al.*, 2003; Niu *et al.*, 2003; Liu *et al.*, 2003). The relationship between plant stomatal conductance and water stresses in soil and air reflected important characteristics of drought resistance and tolerance at leaf level (Costa Franca *et al.*, 2000; Gorio *et al.*, 1999; Sadras & Milroy, 1996; Zavala, 2004). Numerous experiments showed that stomatal conductance responded to humidity (Monteith, 1995; Park & Furukawa, 1999; Haefner *et al.*, 1997), soil water status (Gorio *et al.*, 1999; Liang & Zhang, 1999), water vapor pressure deficit (Turner *et al.*, 1984; Gucci *et al.*, 1996; Franks *et al.*, 1997), and leaf water potential (Gorio *et al.*, 1999; Gucci *et al.*, 1996). Concentrations of some chemical compounds in plant leaves also responded to leaf water stresses, and thus have been used as indicators and parameters for plant drought resistance (Tardieu & Davies, 1993). The complex and nonlinear relationship between stomatal conductance and various controlling factors calls for reliable models of stomatal conductance to summarize data yielded from gas exchange experiments, so as to derive characteristics of drought resistance and tolerance from the data. Reliable, reasonably mechanically based stomatal models are also essential for ecosystem simulation and analysis in order to reduce the risk of extrapolation, so that ecosystem response to future environments can be projected (Gao *et al.*, 2002; Gao & Reynolds, 2003).

With the increasing demands from both experimental data analysis and ecosystem modeling, a number of empirical and mechanical stomatal conductance models have been developed (Ball *et al.*, 1987; Tardieu & Davies, 1993; Leuning, 1995; Gao *et al.*, 2002; Dewar, 2002; Tuzet *et al.*, 2003; Buckley *et al.*, 2003). Not only do these models differ in their assumptions, mathematical formulation and complexities, but also they are validated using different materials in different locations with different experimental conditions. Therefore the differences in their performance and behavior are largely unknown for a particular application. Of these models, the Ball-Berry-Leuning model (also known as BBL model) has been widely applied to various experimental data analysis and ecosystem simulations. The paper doesn't pay more attention to the largely empirical model such as Jarvis model even it had been widely used.

This paper reports the data from field gas exchange experiments of three plant species in a semiarid environment. The BBL stomatal model (Leuning, 1995) and the stomatal conductance model by Gao *et al.* (2002) are

then applied to the experimental data. The behavior and performance of the two models are compared. Drought resistance and tolerance of the plants are then discussed.

1 Material and Methods

1.1 Field measurements and data preparation

Our field experiments were conducted in a small rural watershed of Wufendigou (111° 7' E, 39° 46' N) located in the transitional area between Loess Plateau and Erdos Plateau. The area is also a part of crop-pastoral zone in North China. Annual mean temperature and precipitation are 7.6 °C and 389.8 mm, respectively, based on the local weather data from 1961 to 2000. Annual pan evaporation and mean air humidity, however, are 2 002.5 mm and 53.5%, respectively. Hilly lands with large gullies resulting from long-term serious rainfall erosions are the basic geomorphological features of the area.

Populus simonii, a deciduous broadleaved tree species, *Pinus tabulaeformis*, an evergreen coniferous tree species, and *Caragana intermedia*, a deciduous shrub, are selected as materials for this study, because they are the major species used in local ecosystem conservation and restoration research, and practice. All the three species are classified as C₃ species according to their carbon pathway. For each plant, diurnal leaf stomatal conductance and net assimilation rate, together with microclimate variables such as leaf temperature, incident photon flux density and vapor pressure, were measured every two hours from 8:00 am to 18:00 pm with a portable photosynthesis system (LI-6400, Li-Cor Inc., Lincoln NE, USA) in the sunny day of September, 2003. Soil water contents (g g⁻¹) at depths of 5 - 10, 20 - 30, 50 - 60, 70 - 80, 120 - 130 and 150 - 160 cm near the experimental plants were measured with oven-dry method at 6:00 am. The gravitational soil water contents were multiplied by bulk density to give volumetric soil water content, and soil water potential were then calculated from soil water contents by means of the relationship by Campbell *et al.* (1993). Apparent soil water potential experienced by plants roots are calculated as averages of the water potentials of soil layers weighed by plant root fractions in the layers.

1.2 Models and parameterization

1.2.1 Ball-Berry-Leuning model

The BBL model of stomatal conductance (Leuning, 1995; Ball *et al.*, 1987) reads

$$g_{sc} = g_0 + \frac{aA}{(c_s - c_a)(1 + D_s/D_0)} \quad (1)$$

where g_{sc} was the stomatal conductance for CO₂ diffusion

($\text{mol m}^{-2} \cdot \text{s}^{-1}$), g_0 is the stomatal conductance at the light compensation point ($\text{mol m}^{-2} \cdot \text{s}^{-1}$), A is net CO_2 assimilation rate ($\mu\text{mol m}^{-2} \cdot \text{s}^{-1}$), c_s is the mole fraction of CO_2 at the leaf surface ($\mu\text{mol mol}^{-1}$), Γ is the compensation point ($\mu\text{mol mol}^{-1}$), D_s is the vapor pressure deficit (VPD) (kPa) at the leaf surface, a (unitless) and D_0 (kPa) are constant coefficients.

1.2.2 The stomatal model by Gao *et al.* (2002)

The model by Gao *et al.* was derived based on the mechanics of guard cell structure and water relation of leaves, and was primarily intended for large-scale ecosystem simulation. The model takes the following mathematical form,

$$g_{sw} = \frac{g_{0m} + (k_s + k I_p)/1000}{1 + k_g d_{vp}} \quad (2)$$

where g_{sw} is stomatal conductance to water vapor ($\text{mol m}^{-2} \cdot \text{s}^{-1}$), dividing g_{sw} in (2) by 1.6 gives g_{sc} in (1); g_{0m} is the maximum possible stomatal conductance at dark with zero soil water potential ($\text{mol m}^{-2} \cdot \text{s}^{-1}$); k is the elastic compliance of guard cell structure ($\text{mmol m}^{-2} \cdot \text{s}^{-1} \text{kPa}^{-1}$), ψ_s is soil water potential (kPa), k_s is the parameter defined as changes in stomatal conductance induced by unit changes in PAR ($\text{mmol } \mu\text{mol}^{-1}$), I_p is the incident photosynthetic active radiation ($\mu\text{mol m}^{-2} \cdot \text{s}^{-1}$), k_g is a parameter signifying the sensitivity of stomatal conductance to vapor pressure deficit (unitless), d_{vp} is the relative vapor pressure deficit (kPa kPa^{-1}) calculated as VPD divided by air pressure. Other physiologically significant parameters are derivable using the following relationships: stiffness or elastic modulus of guard cell structure, ($\text{kPa } [\text{mmol m}^{-2} \cdot \text{s}^{-1}]$), is the inverse of k , i. e., $E = 1/k$; Guard cell osmotic sensitivity to light, ($\text{kPa } [\text{mmol m}^{-2} \cdot \text{s}^{-1}]$), is the product of k and I_p , i. e., $\Delta g = k I_p$; soil-to-leaf conductance, g_z ($\text{mmol m}^{-2} \cdot \text{s}^{-1} \text{kPa}^{-1}$), is calculated as the inverse of the product of the elastic modulus and k_g , i. e., $g_z = 1/(k k_g)$; Finally, guard cell osmotic potential at dark, ψ_0 (MPa), is calculated as $\psi_0 = g_{0m}/k$.

Of all these parameters, ψ_0 is the capability for plant to maintain stomatal opening under water stresses. In other words, stomata remain open when soil water potential is higher than ψ_0 , but get closed when soil water potential is lower than ψ_0 . Hence ψ_0 is regarded as a drought tolerance parameter of plants. The elastic compliance of guard cell structure, k , (or elastic modulus E) is the sensitivity of stomatal conductance to incremental soil water stresses. For a given decrease in soil water potential, a larger k (or a smaller E) implies a greater de-

crease in stomatal conductance. Hence k (or E) is regarded as a drought resistance parameter to incremental soil water stress (Gao *et al.*, 2002).

The two models were then applied to the field data by means of nonlinear least square regression. For the BBL model, stomatal conductance is regressed on net assimilation rates (A), leaf surface CO_2 (C_s) and VPD (D) to obtain g_0 , a , and D_0 , with Γ set to $40 \mu\text{mol mol}^{-1}$ (Leuning, 1995). Similarly, stomatal conductance is regressed on incident photon flux density (I_p), soil water potential (ψ_s), and relative vapor pressure deficit (d_{vp}) to obtain g_{0m} , k , k_g and k_s , for the model by Gao *et al.* (2002). The models are then compared in terms of their performance in explanation of the variation in the field gas exchange data. Possible drought resistance and tolerance characteristics of the plants can be obtained.

1.3 Sensitivities of the two models to changes in soil water and vapor pressure

To look into the differences in behavior under variable micro-environmental conditions, we prescribed the following driving climatic and soil conditions for the two models.

$$T_{leaf} = 22.0 + 9.0 \cos\left[\frac{2(t - 14.5)}{24}\right] \quad (3)$$

$$I_p = \max\left\{2000 \cos\left[\frac{2(t - 12)}{24}\right], 100\right\} \quad (4)$$

where T_{leaf} is the leaf temperature ($^{\circ}\text{C}$), t is the time in hour. Thus maximum leaf surface temperature is 31°C occurring at 14:30 pm, and peak incident photon flux density of $2000 \mu\text{mol m}^{-2} \cdot \text{s}^{-1}$ occurs at 12:00 am (solar noon). The concentration at the leaf surface is assumed to a constant of $380 \mu\text{mol mol}^{-1}$. Air pressure is fixed at 88.7 kPa, soil water potential at 0, -500, and -2000 kPa, and vapor pressure at leaf surface at 0.5 and 1.8 kPa.

Because the BBL model describes stomatal conductance as a function of net assimilation rates, we need a model of photosynthesis to calculate carbon assimilation rates from these environmental conditions. The model by Thornely and Johnson (1990), modified by Gao *et al.* (2004), is used for this purpose. We refer this model as the Π model in this paper. The model calculates net assimilation rates as a function of incident photon flux density, leaf temperature and stomatal conductance (Gao *et al.*, 2004):

$$A = \frac{b_1 - \sqrt{b_1^2 + 4b_2b_0}}{2b_2} \quad (5)$$

in which

$$b_2 = P_a(g_{so}g_x - g_{sc}g_p) \quad (6)$$

$$b_1 = g_{sc}g_{so}(I_p + g_x c_s + g_p o_a) - R_d P_a (g_{so}g_x - g_{sc}g_p) + I_p P_a (g_{sc}g_p + g_{so}g_x) \quad (7)$$

$$b_0 = g_{sc}g_{so}[R_d(I_p + g_x c_s + g_p o_a) + I_p(g_p o_a - g_x c_s)] \quad (8)$$

where P_a is atmospheric pressure (kPa), g_{so} is stomatal conductance for O_2 ($\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), g_x is carboxylation conductance ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{kPa}^{-1}$), g_p is photorespiration coefficient ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{kPa}^{-1}$), ϵ is photon efficiency ($\text{mol} \cdot \text{mol}^{-1}$), o_a is atmospheric O_2 partial pressure (kPa), R_d is dark respiration coefficient ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). g_x , g_p , R_d are all functions of leaf temperature:

$$= \epsilon [1 + k_t (T_{leaf} - 20)] \quad (9)$$

$$g_x = g_{x0} [1 + k_t (T_{leaf} - 20)] \quad (10)$$

$$g_p = g_{p0} [1 + k_t (T_{leaf} - 20)] \quad (11)$$

$$R_d = R_{d0} \exp\left(\frac{T_{leaf} - 25}{14.427}\right) \quad (12)$$

where ϵ , g_{x0} and g_{p0} are values of ϵ , g_x , g_p at $T_{leaf} = 20$, R_{d0} is the value of R_d at $T_{leaf} = 25$, and k_t is a temperature coefficient set to 0.05 according to Thornley and Johnson (1990). We obtained the parameters, ϵ , g_{x0} , g_{p0} , and R_{d0} , from the gas exchange data also by means of nonlinear least square regression of net photosynthesis rates on measured incident photon flux density, stomatal conductance, and leaf temperature. Thus the calculations of stomata conductance and net assimilation rate are coupled for the BBL and the Π models. An iteration algorithm is needed to compute net assimilation rate and stomatal conductance simultaneously.

The prescribed micro-environmental conditions were then used to drive the models, and stomatal conductance

was calculated and compared between the two models and among the three species.

2 Result and Discussion

2.1 Parameters of the stomatal conductance models

The results of nonlinear least square regression of stomatal conductance on observed respective independent variables using the two models of stomatal conductance are given in Figure 1 and Table 1 and 2. The regression significant analysis result by F test is provided in Table 1 and 2. Figure 1 compares measured and predicted stomatal conductance (for CO_2) by the two models for the three species. The F -statistics indicates that all the regressions are significant. The BBL model explained 77.5%, 73.6% and 81.8% of variations in diurnal stomatal conductance for *Populus simonii*, *Pinus tabulaeformis* and *Caragana intermedia*, respectively. The variations explained by Cao *et al.* (2002) are 62.7%, 41.7%, and 73.5% respectively. The BBL model explained more variation of the stomatal conductance than the model by Cao *et al.* (2002). This is largely because all variables involved in the BBL model are defined at plant leaf, and net assimilation rate (A) is a better variable to describe the energy available for active osmotic adjustment than incident photon flux density (I_p). The model by Cao *et al.* (2002), however, takes into account the water flow from soil to leaves in addition to the active and passive hydrological feedbacks in the leaves, which is much more complicated than the processes at leaves alone. The tradeoff for using net assimilation rate instead of incident photon flux density as the driving

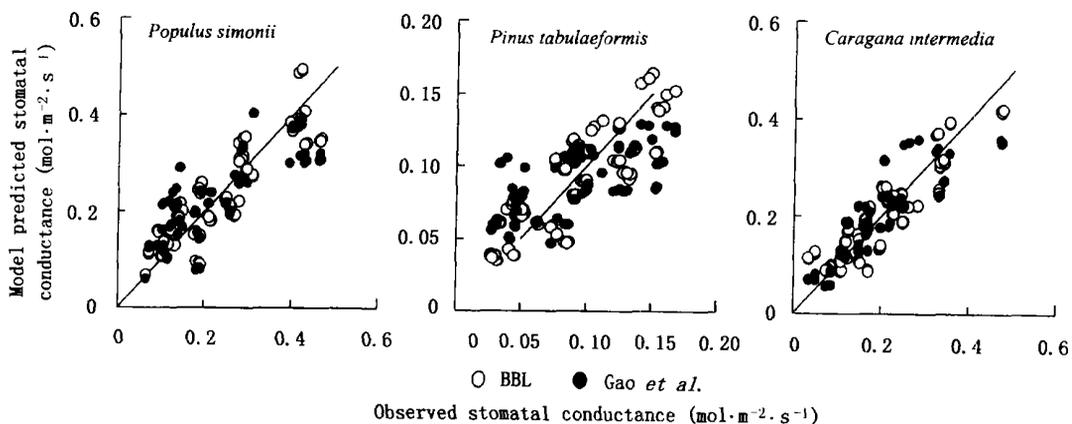


Fig. 1 Comparison of stomatal conductance predicted by the two models

Table 1 Nonlinear regression result for the BBL models

Species	g_0	D_0	R^2	F	$F_c(1\%)$	
<i>Populus simonii</i>	0.074 0	29.99	0.247 1	0.775	$F_{98}^3 = 112.5$	3.99
<i>Pinus tabulaeformis</i>	0.026 5	196.34	0.019 0	0.736	$F_{103}^3 = 97.7$	3.97
<i>Caragana intermedia</i>	0.067 1	10.84	1.179 4	0.818	$F_{98}^3 = 147.0$	3.99

Table 2 Nonlinear regression result for the model by Gao *et al.* (2002)

Species	g_{0m}	k	k_g	k_e	R^2	F	$F_c(1\%)$	g_z		
<i>Populus simonii</i>	0.77	0.37	1.19	253.5	0.627	$F_{98}^4 = 37.1$	3.52	2.7	-2.06	0.0015
<i>Pinus tabulaeformis</i>	1.47	0.13	0.73	600	0.416	$F_{105}^4 = 14.2$	3.50	7.4	-10.9	0.0002
<i>Caragana intermedia</i>	5.19	0.51	16.35	2320.9	0.735	$F_{98}^4 = 66.6$	3.52	2.0	-10.2	0.0002

variable for stomatal conductance is that it requires an iterative algorithm to compute net assimilation rate and stomatal conductance simultaneously in the BBL model. Not only does an iterative algorithm consume tens or hundreds times more computer resources than a non-iterative one, but also the convergence problem associated with iterative computation quite often makes the simulation impossible.

Table 1 indicates that the values of g_0 and D_0 for *Pinus tabulaeformis* are much lower than those for the other species. This means the stomatal conductance at light compensation point is lower, and the stomatal conductance of the species is more sensitive to changes in air vapor pressure, than the other species.

The value of k for the pine tree is much higher than other species. This indicates either more assimilated energy spent on stomatal opening, or the active hydrological osmotic adjustment are more sensitive to assimilated energy, or both, for the pine.

Table 2 illustrates the estimated parameters of Gao *et al.* (2002). The shrub *Caragana intermedia* and the pine have lower dark osmotic potential (g_0), thus have greater tolerance for water stresses, than the deciduous broadleaved poplar tree. The *Caragana* shrub and the poplar tree, however, have larger guard cell compliance (k), or smaller guard cell modulus (k_g), thus are more sensitive to increases in soil water stress, than the pine. Hence the poplar tree is the least tolerant for and resistant to soil water stresses. The pine tree is more tolerant for soil water stresses but less sensitive to incremental soil water stresses, than the other two species. This result means that the pine tree can maintain physiologically active at severe water stresses, but may also lose water by means of large transpiration, thus may not be good for soil water conservation. The *Caragana* shrub, however, has

both higher tolerance and larger sensitivity to incremental soil water stresses than the other species, hence can give large stomatal conductance for carbon assimilation when soil is wet, and conserve water at severe soil water stress. These findings are consistent with those found in Gao *et al.* (2002) and also in a number of experimental studies (Dong & Zhang, 2001; Monson & Smith, 1982; Nilsen *et al.*, 1983). The *Caragana* shrub also has the largest k , thus is more sensitive to light intensity than the trees.

2.2 Stomatal conductance under prescribed soil and micro-climatic conditions

Figure 2 gives the simulated stomatal conductance with the two models under prescribed scenarios with different soil water potential and air vapor pressures, but with a common diurnal temperature and light conditions. Both models give larger stomatal conductance in the morning but smaller values in the afternoon. The calculated stomatal conductance with the model by Gao *et al.* (2002) is in general smaller than that with the BBL model. Both models have similar sensitivities to changes in vapor pressure. The most distinct difference between the two models, however, is their responses to changes in soil water potential. The model by Gao *et al.* (2002) responds to changes in soil water stresses. The response of the poplar tree is especially evident because it has the smallest tolerance for and resistance to soil water stresses. The responses of the pine tree and the shrub are not so strong because these two species are either much more tolerant for or resistant to increases in soil water stresses. In contrast, the couple BBL-TJ model does not respond to soil water stresses at all. Hence the BBL model may not be appropriate for experimental data analysis and ecosystem simulation in arid and semi-arid regions.

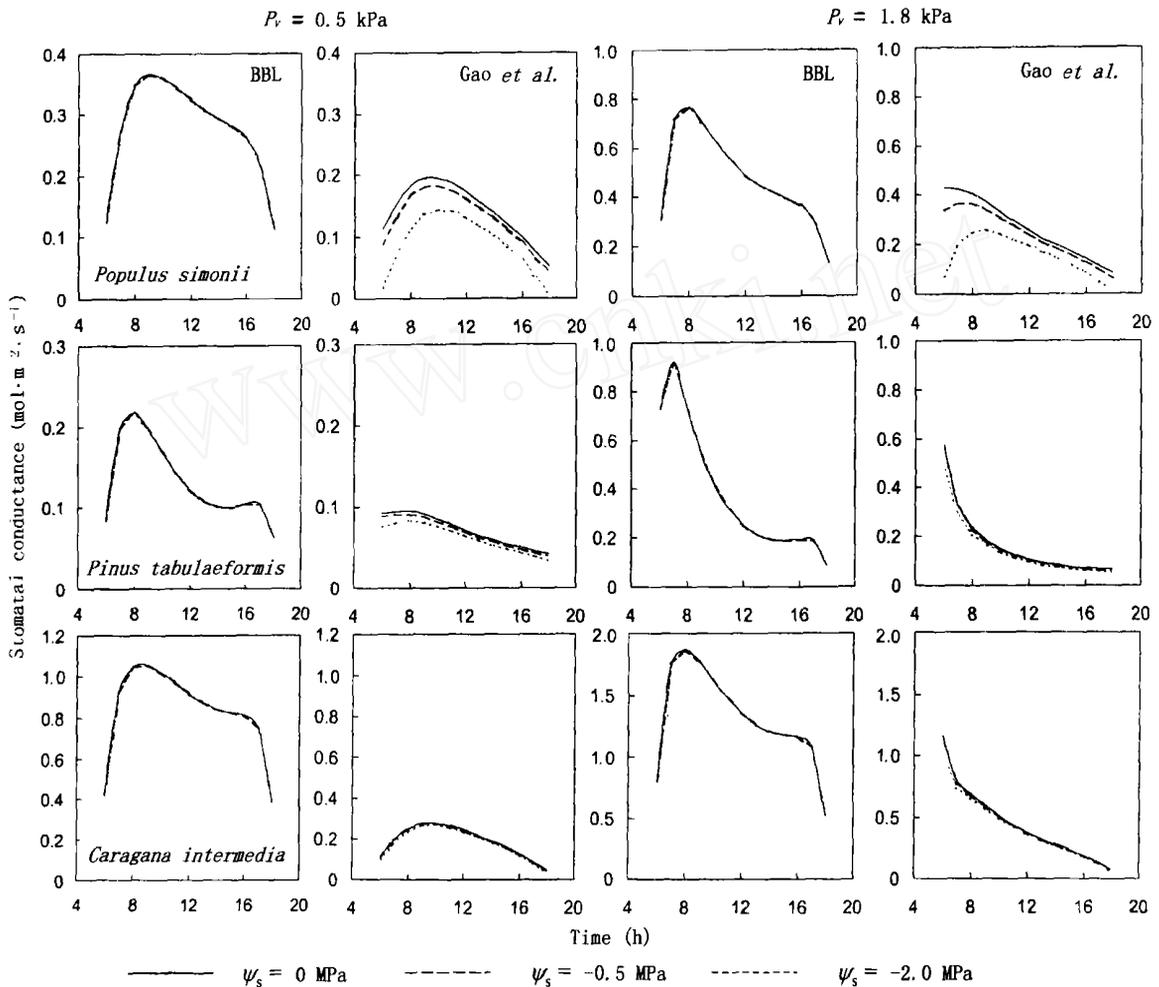


Fig. 2 Simulated stomatal conductance by the two models under prescribed micro-environmental conditions

3 Conclusion

Our goal was to test, compare the BBL model and the Gao model using the data from field gas exchange experiments of three plant species in a semi-arid environment. The nonlinear regression result indicated that the BBL model and the Gao model could explain on average 77.6% and 59.3% of variations in the observed stomatal conductance respectively. The BBL model explained more variation of the stomatal conductance than the Gao model. This was largely because all variables involved in the BBL model were defined at the plant leaf.

The BBL model tended to give higher predictions to stomatal conductance than the Gao model under prescribed soil and micro-climate conditions. The sensitivity analysis showed the responses of the two models were similar to changes in vapor pressure. The sharp contrast between the two models, however, was that the Gao model responded to changes in soil water stress to different extents while the BBL model coupled with Γ photosynthesis model was indifferent to the increases of soil water stress-

es. Thus the BBL model, even though with its better explanations of the variations in field stomata data, may not be appropriate for experimental data analysis and applications for ecosystems simulation.

The analysis using the Gao model indicates that *Populus simonii* was the least tolerant for and resistant to water stresses among the three species studied. *Pinus tabulaeformis* had both high tolerance and resistance than other species, but the stomatal conductance of the pine tree is the least insensitive to changes in soil water stresses. Hence the pine tree may not be good for water conservation under extremely dry conditions. *Caragana intermedia*, however, had both larger drought tolerance and larger sensitivity to incremental soil water stresses than the other species, thus can provide large stomatal conductance for photosynthesis when soil water stress was low, and conserve soil water stress.

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