**Full Length Article**

# Characteristics and Quantitative Simulation of Stomatal Conductance of *Panax notoginseng*

**Chao Xu[1], Zaiqiang Yang[1*], Mingtian Wang[2*], Xuran Zhang[1], Qiantong Zheng[1], Jiajia Li[1], Floribert Vuguziga[1] and Yujia Zou[3]**

[1]*Collaborative Innovation Center on Forecast and Evaluation of Meteorological Disasters, Nanjing University of Information Science and Technology, Nanjing 210044, Jiangsu Province, P.R. China*

[2]*Sichuan Meteorological Observatory, Chengdu 610031, Sichuan Province, P.R. China*

[3]*Sichuan Agricultural Meteorological Center, Chengdu 610031, Sichuan Province, P.R. China*

*For correspondence: yzq@nuist.edu.cn; wangmt0514@163.com

## Abstract

In order to construct a mathematical model for response of stomatal conductance (gs) of *Panax notoginseng* (Burk.) F.H.Chen leaves to environmental factors. Three-year-old *P. notoginseng* seedlings were used as experimental materials. The daily variation of gs and environmental factors of *P. notoginseng* leaves in sunny and cloudy days was determined by LiCOR-6400 Infra-Red Gas Analyzer (IRGA) in September and October 2018. The stepwise regression method was used to analyze the response of gs of *P. notoginseng* leaves to environmental factors, and the optimal gs model of *P. notoginseng* leaves were simulated and verified by using two types of representative stomatal conductance models. The results showed that the daily variation of gs showed a double-peak curve in sunny days, while in cloudy days showed a single-peak curve. Photosynthetically active radiation (PAR), vapor pressure deficit (VPD) and air temperature ($T_{air}$) were the main environmental factors affecting gs, in which PAR and $T_{air}$ were positively correlated with gs, while VPD was negatively correlated. The best fitting effect of gs of *P. notoginseng* leaves was Jarvis model 1, followed by Jarvis model 2 and Ball-Berry model 2, and finally Ball-Berry model 1. The fitting effect of each model in the afternoon was better than that in the morning. Therefore, the optimal response model of gs of *P. notoginseng* leaves to environmental factors was established, which was:

$$g_s = \frac{200.12 PAR(1-0.312 VPD)(1.347-0.086T+0.002T^2)(1-0.002C_a)}{(121.36+PAR)(1+12.75 VPD)} \cdot$$

This model not only helped to further estimate leaf photosynthesis, but also laid the foundation for simulating water and heat exchange in the soil-plant-atmosphere systems. © 2019 Friends Science Publishers

**Key words:** Ball-Berry model; Environmental factors; Jarvis model; *P. notoginseng*; Stomatal conductance

## Introduction

Stomata are the main channel for water and gas exchange between terrestrial plants and the environment, and are also an important regulatory channel for material and energy exchange between soil-plant-atmosphere continuum (SPAC) in nature (Hetherington and Woodward, 2003; Bonan *et al*., 2014). The degree of opening and closing of the stomata is usually expressed by the stomatal conductance (gs), which is related to the net photosynthetic rate and the $CO_2$ concentration (Buckley, 2007; Damour *et al*., 2010). The gs is an important factor in determining plant photosynthesis and transpiration intensity (Miner *et al*., 2017). An accurate and quantitative description of plant stomatal response to the environment is a key to understand the plant photosynthesis and plant transpiration; and to predict the plant productivity, water and heat exchange within SPAC.

Numerous studies reported on the relationship between gs and environmental factors in plant leaves (Bernacchi *et al*., 2007; Igarashi *et al*., 2015; Sperry *et al*., 2017; Urban *et al*., 2017). Bunce (2000) revealed that under natural conditions, gs is affected by photosynthetically active radiation (PAR), vapor pressure deficit (VPD) and air temperature ($T_{air}$). Wang *et* al (2016) indicated that gs is regulated by different environmental factors in different periods. PAR, VPD and $T_{air}$ have the most significant effects on gs during the whole day and morning, while gs in the afternoon is also affected by $CO_2$ concentration (Ca) and relative humidity (RH). The abscisic acids (ABA) in xylem sap and leaf water potential are also involved in stomatal control, and different species have different effects (Tardieu and Davies, 1993; Buckley and Mott, 2002). Some studies have shown that when the environmental response mechanism of stomata is not well understood, model simulation becomes the most effective and appropriate tool (Buckley, 2017).

The gs model is an important tool for evaluating stomatal regulation in plant leaves. There are two main models for describing the relationship between gs and environmental factors in plant leaves: (1) the multivariate nonlinear model of stomatal conductance and environmental factors established by Jarvis (Jarvis, 1976); and (2) the linear correlation model of stomatal conductance and net photosynthetic rate with environmental factors established by Ball (Ball *et al.*, 1987; Ball, 1988).

The Jarvis model is a typical factorial empirical model, which is a function of a series of single factor correction coefficients, but parameters in Jarvis model do not have a clear physiological significance, which changes with the specific plot or variety (Calvet, 2000). The Ball model (Ball, 1988) is a semi-empirical model based on experimental data that considers a linear relationship between gs and net photosynthetic rate. Based on the Ball model, different forms of gs correction models are presented such as Ball-Woodrow-Berry model (BWB) model (Ball *et al.*, 1987) and Ball-Berry-Leuning (BBL) model (Leuning, 1995), but the essence of these modified models is still the Ball-Berry (BB) model. In terms of the applicability of these two models, a large number of experiments have been carried out on crops (Yu *et al.*, 2001). However, the fitting ability of the two models has certain differences depending on the research objective and the regional environmental conditions (Gao *et al.*, 2016).

*Panax notoginseng* (Burk.) F.H.Chen has a long history as a traditional Chinese herbal medicine (Tung and Hai, 2016). The growth conditions of *P. notoginseng* are harsh. For a long time, the cultivation of *P. notoginseng* is limited by temperature, humidity, sunshine and other external climatic conditions so the greenhouse cultivation of *P. notoginseng* will become the main trend. In the process of planting *P. notoginseng* in greenhouse, it is an important way to improve water use efficiency to regulate the environment according to the physiological needs of *P. notoginseng*. Therefore, studying the influence of environmental factors on stomatal conductance of *P. notoginseng* is helpful to explain the water use mechanism of *P. notoginseng* and optimize environmental management. At present, the relationship between gs and environmental factors of *P. notoginseng* leaves and the numerical simulation of gs have rarely been reported. This paper will attempt to analyze the main environmental factors affecting the gs of *P. notoginseng* leaves based on field observation. Two types of representative international gs models were compared to establish an optimal gs model suitable for the *P. notoginseng* leaves.

## Materials and Methods

### Experiment Location and Materials

The experiment was conducted in Venlo-type glasshouse of the Agricultural Meteorological Experiment Station of Nanjing University of Information Science and Technology from September to October 2018, Jiangsu Province, China (32°14'N, 118°42'E). The Venlo-type glasshouse, with a north-south length of 30 m, is composed of 12 spans, each 6 m wide in the east-west direction. The height of gutter and ridge was 4 m and 4.73 m, respectively.

The experiment materials were three-year-old sanchi seedlings (*Panax notoginseng* (Burk.) F.H. Chen) grown in pots (40 cm × 20 cm × 20 cm) provided by farmers in Qiubei County, Wenshan Prefecture, Yunnan Province. The seedlings height was 18–20 cm and the number of leaves was 6–10. The pots were filled with Humus-rich red loam soil, its pH value was 6.5, and the soil water content was always maintained at 35–40%, which were the most suitable conditions for the growth of *P.notoginseng* seedlings.

### Measurements

**Meteorological data collection**: The environmental data was collected by the automatic data collector (CR-10X, USA), and the air temperature ($T_{air}$) and humidity (RH) at 1.5 m from the ground and the photosynthetically active radiation (PAR, $\mu mol \cdot m^{-2} \cdot s^{-1}$) above the canopy of the crop were collected. The frequency was 1 time every 10 s, and the average value was stored every 30 min.

**Determination of stomatal conductance:** In September, typical sunny days (3 days) and cloudy days (3 days) were selected as observation days, and repeated the above determination in October. Design of the experiments was completely randomized with three replications. Healthy, non-destructive leaves were selected for determination, with each leaf repeated five times each time. The portable Infra-Red Gas Analyzer (LI-COR Inc., Lincoln, NE, USA) was used to measure the photosynthetic parameters on hourly basis from 8:00 am to 18:00 pm. The parameters recorded were net photosynthetic rate ($P_n$, $mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (gs, $mol \cdot m^{-2} \cdot s^{-1}$), air $CO_2$ concentration ($C_a$, $\mu mol \cdot mol^{-1}$), intercellular $CO_2$ concentration ($C_i$, $\mu mol \cdot mol^{-1}$), and Vapor Pressure Deficit (VPD, kPa). The data measured in September was used for the establishment of the model, and the data for October was used for the verification of the model. This study does not consider the effect of leaf water potential on gs.

### Stomatal Conductance Model Description

**Jarvis model:** Jarvis (1976) considers that stomatal conductance is the product of the combined action of several environmental factors. The comprehensive effect of multiple environmental factors on leaf stomatal conductance can be obtained by superposition of stomatal conductance response to a single environmental factor. The specific form of the model was as follows,

$$gs = gs(PAR)f(VPD)f(\varphi)f(T)f(C_a) \qquad (1)$$

Where gs is stomatal conductance, while gs (PAR), f(VPD), f($\varphi$), f(Ta), and f(Ca) are response functions of photosynthetic active radiation, saturated water vapor pressure difference, leaf water potential, temperature and $CO_2$ concentration to

stomatal conductance, respectively. PAR is the dominant factor determining stomatal conductance, while f(VPD), f(φ), f(Ta), f(Ca) mainly revise gs (PAR) with the values ranging from 0 to 1.

When constructing the Jarvis model, there are many expressions for the influence functions of each factor (Medlyn *et al.,* 2011). Different expressions contain different numbers of parameters, which leads to differences in the complexity and prediction effects of the model. In order to compare models with different degrees of complexity, two different response function expressions were selected in this study. The first group contains 8 parameters, and the corresponding model is called Jarvis model 1 while the second group contains 4 parameters, the corresponding model is called Jarvis model 2.

The Influence function of each environmental factor in Jarvis model 1 was expressed as:

$$g_s(PAR) = \frac{a_1 PAR}{a_2 + PAR} \qquad (2)$$

$$f(VPD) = \frac{1 - b_1 VPD}{1 + b_2 VPD} \qquad (3)$$

$$f(T) = c_1 + c_2 T + c_3 T^2 \qquad (4)$$

$$f(C_a) = 1 - d_1 C_a \qquad (5)$$

The Influence function of each environmental factor in Jarvis model 2 was expressed as:

$$g_s(PAR) = \frac{PAR}{a + PAR} \qquad (6)$$

$$f(VPD) = \frac{1}{b + VPD} \qquad (7)$$

$$f(T) = cT^2 \qquad (8)$$

$$f(C_a) = 1 - dC_a \qquad (9)$$

Where, $a_1$, $a_2$, $b_1$, $b_2$, $c_1$, $c_2$, $c_3$, $d_1$, a, b, c and d are model parameters. Therefore, Jarvis Model 1 and Jarvis Model 2 are Eqs. (10) and (11), respectively.

$$g_s = \frac{a_1 PAR(1 - b_1 VPD)(c_1 + c_2 T + c_3 T^2)(1 - d_1 C_a)}{(a_2 + PAR)(1 + b_2 VPD)} \qquad (10)$$

$$g_s = \frac{PAR c T^2 (1 - dC_a)}{(a + PAR)(b + VPD)} \qquad (11)$$

**Ball-berry model:** (Ball *et al.,* 1987): When $CO_2$ concentration and atmospheric humidity are constant; the stomatal conductance has a linear relationship with the net photosynthetic rate. Ball and Berry proposed the following linear stomatal conductance model.

$$g_s = \frac{m A_n h_s}{C_s} + b \qquad (12)$$

Where, $A_n$ is the net photosynthetic rate; $h_s$ and $C_s$ are the atmospheric relative humidity and the leaf surface $CO_2$ concentration, respectively; m and b are the empirical coefficients, while $A_n h_s / C_s$ is the stomatal conductance index. However, due to the poor prediction ability of the Ball-Berry model at low $CO_2$ concentration, Leuning (1995) revised the Ball-Berry model.

$$g_s = \frac{m A_n}{(C_s - \Gamma)(1 + VPD_s / VPD_0)} + g_{s0} \qquad (13)$$

Where, m, $VPD_0$, and $g_{s0}$ are model parameters; $\Gamma$ is the $CO_2$ compensation point, which varies with different varieties.

**Performance of Stomatal Conductance Models**

The experimentally segregated data were fitted using Sigmaplot 12.5 (SYSTAT Software, USA) to determine model parameters, give fitness ($R^2$) and significance ($P \leq 0.01$). The simulation effects of each model were evaluated by root mean square error (RMSE), model slope ($b_0$), and Akaike information criterion (AIC). The calculation formulas for RMSE, $b_0$ and AIC are respectively described as follow:

$$RMSE = \sqrt{\frac{\sum_1^n (O_i - M_i)^2}{n}} \qquad (14)$$

$$b_o = \frac{\sum_{i=1}^n O_i M_i}{\sum_{i=1}^n O_i^2} \qquad (15)$$

$$AIC = n \ln \frac{\sum_1^n (O_i - M_i)^2}{n} + 2(k+1) \qquad (16)$$

Where, $O_i$ represents the measured value; $M_i$ represents the observed value; n is the number of samples; k is the number of parameters in the model. The smaller the RMSE value, the better the simulation effect; the model slope $b_0$ reflects the overestimation or underestimation of the model. When $b_0 > 1$, it means an overestimation, and $b_0 < 1$ means underestimation; the closer to 1, the better the simulation effect; AIC can estimate the complexity of the model and the pros and cons of the model fitting effect. The smaller the value, the better the simulation effect of the model.

## Results

### Diurnal Variation of gs in Leaves of *P. notoginseng*

The daily variation of gs in the leaves of *P. notoginseng* on sunny and cloudy days is shown in Fig. 1. On sunny days, the daily variation of gs in leaves of *P. notoginseng* showed a bimodal curve, reaching the maximum at 11:00 am and 15:00
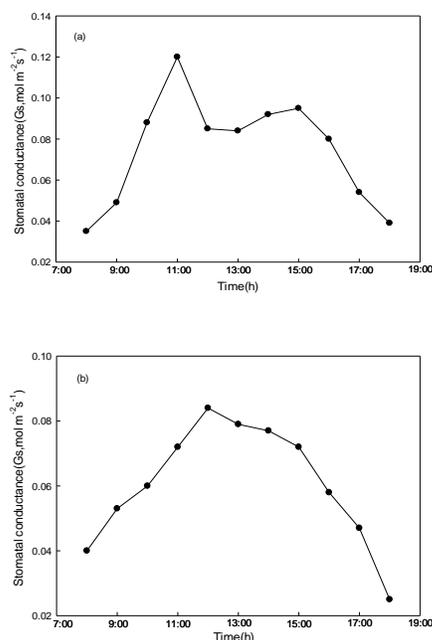
**Fig. 1:** The diurnal variation of stomatal conductance of *P. notoginseng* leaves on (a) sunny day and (b) cloudy day

pm, respectively, and the maximum value in the morning was greater than the maximum in the afternoon. On cloudy days, the daily variation of gs in leaves of *P. notoginseng* showed a single-peak curve, reaching the maximum at 11: 00 am, and then continued to decline.

**Relationship between gs of *P. notoginseng* Leaves and Environmental Factors based on the Analyzed Data**

When PAR<400 μmol·m$^{-2}$ s$^{-1}$, the gs increased with the increase of PAR. When PAR>400 μmol·m$^{-2}$ s$^{-1}$, the gs decreased (Fig. 2a). The gs increased with an increase of Ci, and gradually decreased to about 400 μmol·mol$^{-1}$ s$^{-1}$, and the two showed a quadratic curve relationship (Fig. 2b). The gs increased with the increase of VPD within a certain range. When VPD reached about 1 kPa, gs reached the highest value, and then gs decreased with the increase of VPD (Fig. 2c). The gs of *P. notoginseng* leaves increased with the increase of $T_{air}$, reached the maximum at around 25°C, and then gradually decreased with the increase of $T_{air}$ (Fig. 2d). The gs increased with the increase of RH, reached the maximum at about 49%, and then gradually decreased with an increase in RH. When RH is between 40% and 55%, the value of gs was the largest (Fig. 2e).

**Impact of Main Environmental Factors**

The regression equation of gs of *P. notoginseng* leaves and various environmental factors is shown in Table. 1 (P<0.01). The most significant environmental factors affecting gs of *P. notoginseng* leaves were PAR, VPD and $T_{air}$.
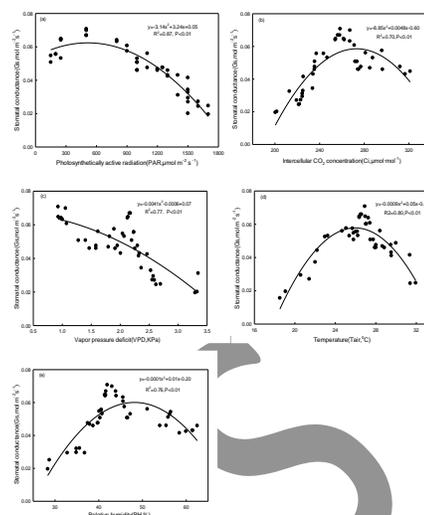


**Fig. 2:** The relationship between stomatal conductance of *P. notoginseng* leaves and environmental factors

Among them, gs was one hand positively correlated with PAR and $T_{air}$, while negatively correlated with VPD.

**gs Model of *P. notoginseng* Leaves**

The simulation results of each model are in Table 2, and all models pass the significance test (P＜0.01). The accuracy of fitting gs of *P. notoginseng* leaves in the afternoon was higher than that in the morning. Overall, the accuracy of Jarvis model was higher than that of Ball-Berry model.

A linear relationship between the simulated and observed values of each model was shown in Fig. 4. The results of model simulation showed that Jarvis model 1 had the highest $R^2$ (0.93), followed by Jarvis model 2 (0.90) and Ball-Berry model 2 (0.87), and Ball-Berry model 1 (0.80) had the lowest.

**Performance of Four gs Models**

The evaluation index of simulation effect of each model is shown in Table 3. From the RMSE, $b_0$ and ACI, it can be seen that the fitting effect of each model in the afternoon was better than that in the morning. In general, the fitting effect of Jarvis model in each period was better than that of Ball-Berry model.

**Discussion**

Stomata play a role of balance regulation in plants and are the key link in regulating the exchange of substance and energy between soil-plant-atmosphere-continuum (Gao *et al.,* 2016). It is the basis for exploring the dynamics of energy and water exchange in plants to clarify the relationship between gs of leaves and the environmental factors. Wang *et al.* (2001) showed that the stomatal conductance of *Aneurolepidium chinense* leaves is very significant in response to PAR, VPD

**Table 1:** Response of stomatal conductance of *P. notoginseng* leaves to environmental factors

| Time | | Regression equation | Number of samples | F value | Significant environmental variables | Correlation coefficient(r) |
|---|---|---|---|---|---|---|
| Sunny day | whole day | gs= -0.218-0.077Vpd+0.15$T_{air}$+0.552PAR | 309 | 128.526 | Vpd, $T_{air}$ and PAR | 0.775** |
| | morning | gs= -0.076-1.992Vpd+0.933$T_{air}$+1.183PAR | 137 | 33.378 | Vpd, $T_{air}$ and PAR | 0.855** |
| | afternoon | gs=0.012+0.005Ci-1.127Vpd+0.443$T_{air}$+0.598PAR | 172 | 106.533 | Ci, Vpd, $T_{air}$ and PAR | 0.810** |
| Cloudy day | whole day | gs= -0.151-1.512Vpd+0.968$T_{air}$+0.473PAR | 318 | 63.428 | Vpd, $T_{air}$ and PAR | 0.786** |
| | morning | gs= -0.23-2.438RH-6.074Vpd+4.251$T_{air}$+0.784PAR | 135 | 121.156 | RH, Vpd, $T_{air}$ and PAR | 0.824** |
| | afternoon | gs= 0.146+0.379Ci-2.231RH-5.553Vpd+2.989$T_{air}$+1.208PAR | 183 | 44.804 | Ci, RH, Vpd, $T_{air}$ and PAR | 0.708** |
| Total | whole day | gs= -0.042-1.314Vpd+0.695$T_{air}$+0.534PAR | 627 | 145.038 | Vpd, $T_{air}$ and PAR | 0.888** |
| | morning | gs= -0.055-1.365Vpd+0.806$T_{air}$+0.454PAR | 272 | 46.065 | Vpd, $T_{air}$ and PAR | 0.778** |
| | afternoon | gs= -0.196-1.122Vpd+0.970$T_{air}$+0.554PAR | 355 | 127.190 | Vpd, $T_{air}$ and PAR | 0.722** |

**denotes the significant difference at the 0.01 level

**Table 2:** Estimated parameters at Jarvis and Ball-Berry models

| Model | Time | Parameter values of simulation | Correlation coefficient( r) |
|---|---|---|---|
| Jarvis model 1 | whole day | $a_1$=200.12, $a_2$=121.36, $b_1$=0.312, $b_2$=12.75, $c_1$=1.347, $c_2$=-0.086, $c_3$=0.002, $d_1$=0.002 | 0.897** |
| | morning | $a_1$=186.46, $a_2$=132.16, $b_1$=0.286, $b_2$=10.45, $c_1$=2.556, $c_2$=-0.096, $c_3$=0.003, $d_1$=0.002 | 0.778** |
| | afternoon | $a_1$=218.33, $a_2$=101.26, $b_1$=0.455, $b_2$=15.42, $c_1$=1.198, $c_2$=-0.077, $c_3$=0.001, $d_1$=0.004 | 0.802** |
| Jarvis model 2 | whole day | a=144.32,b=-0.567,c=0.003,d=0.003 | 0.809** |
| | morning | a=165.32,b=-0.698,c=0.002,d=0.001 | 0.756** |
| | afternoon | a=123.89,b=-0.435,c=0.004,d=0.005 | 0.779** |
| Ball-Berry model 1 | whole day | m=0.078,b=0.322 | 0.752** |
| | morning | m=0.085,b=0.268 | 0.698** |
| | afternoon | m=0.634,b=0.421 | 0.701** |
| Ball-Berry model 2 | whole day | m=6825.31, $VPD_0$=0.001, and $g_{s0}$=0.023 | 0.789** |
| | morning | m=6678.59, $VPD_0$=0.003, and $g_{s0}$=0.031 | 0.756** |
| | afternoon | m=7035.12, $VPD_0$=0.002, and $g_{s0}$=0.014 | 0.773** |

**denotes the significant difference at the 0.01 level

and $T_{air}$. Our results showed that PAR, VPD and $T_{air}$ were the main environmental factors affecting stomatal conductance, in which PAR and $T_{air}$ were positively correlated with gs, while VPD was negatively correlated, which were not only consistent with previous conclusions from other plants (Running and Coughlan, 1988; Roberntz and Stockfors, 1998; Li *et al.*, 2010; Wang *et al.*, 2016) but also in line with the assumptions of the Jarvis model (Jarvis, 1976).

The Jarvis model and the Ball model are the two most representative types of gs models. The results of this study showed that Jarvis Model 1 has the highest prediction accuracy, followed by Jarvis Model 2 and Ball Model 2, and finally Ball Model 1. The Jarvis model 1 has the largest number of parameters and the Ball model 1 has the fewest. The Jarvis model 1 with the most parameters has the best prediction effect on the *P. notoginseng* stomatal conductance, while the Jarvis model 2 with the least parameter has the worst prediction effect (Table 2). In the two Ball models, the prediction of the Leuning modified Ball model is better than the original Ball model. The results of this study are consistent with previous studies on other plants (Wang *et al.*, 2001; Tang *et al.*, 2008; Wang *et al.*, 2016). In addition, the linear relationship between gs and $P_n$ was a prerequisite for the construction of the Ball model (Ball *et al.*, 1987). In this study, there was a significant positive correlation between gs and $P_n$ in *P. notoginseng*, but it was a quadratic curve (Fig. 4), which was inconsistent with the mechanism of Ball model construction, which resulted in the Ball model that is not fitting better than the Jarvis model. In the study related to the conductance of *P. notoginseng*, it is recommended to use Jarvis model for simulation.
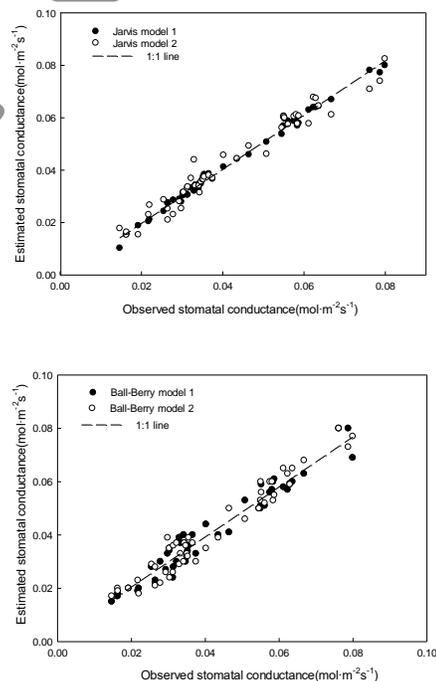




**Fig. 3:** Comparison of estimated and measured values of stomatal conductance of *P. notoginseng* leaves

In the actual application process, the parameters of the model will vary according to the region, variety, growth period and water supply. Therefore, it needs to be revised according to the actual situation. Although Jarvis Model 1 has the best

**Table 3:** Performance of Jarvis and Ball-Berry models

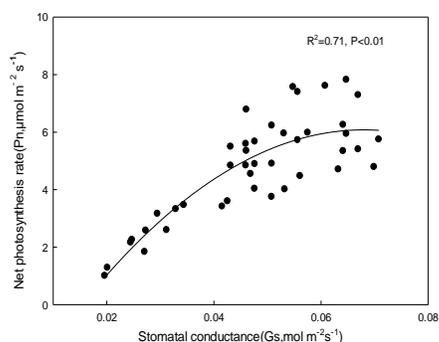| Model | Time | Root mean square error (RMSE) | Model slope ($b_0$) | Akaike information criterion (AIC) |
|---|---|---|---|---|
| Jarvis model 1 | Whole day | 0.0885 | 0.986 | -183 |
| Jarvis model 2 | Whole day | 0.0861 | 0.953 | -200 |
| Ball-Berry model 1 | Whole day | 0.0661 | 0.901 | -244 |
| Ball-Berry model 2 | Whole day | 0.0752 | 0.923 | -231 |



**Fig. 4:** The relationship between net photosynthesis rate and stomatal conductance

prediction effect, the number of parameters is large and no specific biological significance, so it is more difficult to revise the parameters when extended to other regions and varieties.

## Conclusion

The response of gs of *P. notoginseng* leaves to environmental factors remains unclear. Based on the measured data, the main environmental factors affecting stomatal conductance of *P. notoginseng* leaves were determined, and the response model of stomatal conductance to the main environmental factors in different periods of sunny and cloudy days was constructed. The optimal stomatal conductance model of *P. notoginseng* leaves was established by comparing the two types of representative models in the world, which was:

$$g_s = \frac{200.12\text{PAR}(1-0.312\text{VPD})(1.347\text{-}0.086\text{T}+0.002\text{T}^2)(1-0.002\text{C}_a)}{(121.36+\text{PAR})(1+12.75\text{VPD})}$$

This model not only helped to further estimate leaf photosynthesis, but also laid the foundation for simulating water-heat exchange between soil-plant-atmosphere systems.

## Acknowledgements

## References

Ball, J.T., 1988. *An Analysis of Stomatal Conductance*. Dissertation, Stanford University, California, USA

Ball, J.T., I.E. Woodrow and J.A. Berry, 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. *In*: *Progress in Photosynthesis Research*, pp: 221–224. Springer, Dordrecht, Holland

Bernacchi, C.J., B.A. Kimball, D.R. Quarles, S.P. Long and D.R. Ort, 2007. Decreases in stomatal conductance of soybean under open-air elevation of [$CO_2$] are closely coupled with decreases in ecosystem evapotranspiration. *Plant Physiol.*, 143: 134–144

Bonan, G.B., M. Williams, R.A. Fisher and K.W. Oleson, 2014. Modeling stomatal conductance in the earth system: linking leaf water-use efficiency and water transport along the soil–plant–atmosphere continuum. *Geosci. Model Dev.*, 7: 2193–2222

Buckley, T.N., 2007. The role of stomatal acclimation in modelling tree adaptation to high $CO_2$. *J. Exp. Bot.*, 59: 1951–1961

Buckley, T.N. and K.A. Mott. 2002. Stomatal water relations and the control of hydraulic supply and demand. *In*: *Progress in Botany*, pp: 309–325. Springer, Berlin Heidelberg, Germany

Buckley, T.N., 2017. Modeling stomatal conductance. *Plant Physiol.*, 174: 572–582

Bunce, J.A., 2000. Responses of stomatal conductance to light, humidity and temperature in winter wheat and barley grown at three concentrations of carbon dioxide in the field. *Global Change Biol.*, 6: 371–382

Calvet, J., 2000. Investigating soil and atmospheric plant water stress using physiological and micrometeorological data. *Agric. For Meteorol.*, 103: 229–247

Damour, G., T. Simonneau, H. Cochard and L. Urban, 2010. An overview of models of stomatal conductance at the leaf level. *Plant Cell Environ.*, 33: 1419–1438

Gao, G.L., X.Y. Zhang, Z.Q. Chang, T.F. Yu and H. Zhao, 2016. Environmental response simulation and the up-scaling of plant stomatal conductance. *Acta Ecol. Sin.*, 36: 1–10

Hetherington, A.M. and F.I. Woodward, 2003. The role of stomata in sensing and driving environmental change. *Nature*, 424: 901–908

Igarashi, Y., T.O. Kumagai, N. Yoshifuji, T. Sato, N. Tanaka and K. Tanaka, 2015. Environmental control of canopy stomatal conductance in a tropical deciduous forest in northern thailand. *Agric. For. Meteorol.*, 202: 1–10

Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. R. Soc. Lond. B.*, 273: 593–610

Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for $C_3$ plants. *Plant Cell Environ.*, 18: 339–355

Li, X.Y., P.L. Yang, S.M. Ren and L. Ren, 2010. Characteristics and simulation of canopy conductance of cherry. *Acta Ecol. Sin.*, 30: 300–308

Medlyn, B.E., R.A. Duursma, D. Eamus, D.S. Ellsworth, I.C. Prentice, C.V. Barton, K.Y. Crous, P. De Angelis, M. Freeman and L. Wingate, 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biol.*, 17: 2134–2144

Miner, G.L., W.L. Bauerle and D.D. Baldocchi, 2017. Estimating the sensitivity of stomatal conductance to photosynthesis: A review. *Plant Cell Environ.*, 40: 1214–1238

Roberntz, P. and J. Stockfors, 1998. Effects of elevated $CO_2$ concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees. *Tree Physiol.*, 18: 233–241

Running, S.W. and J.C. Coughlan, 1988. A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Model.*, 42: 125–154

Sperry, J.S., M.D. Venturas, W.R. Anderegg, M. Mencuccini, D.S. Mackay, Y. Wang and D.M. Love, 2017. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. *Plant Cell Environ.*, 40: 816–830

Tang, F.D., Y.X. Wu, S.J. Han and J.H. Zhang, 2008. Relationship of stamatal conductance of leaf with environmental factors in broadleaved Korean pine forest at Changbai Mountain. *Acta Ecol. Sin.*, 28: 5649–5655

Tardieu, F. and W.J. Davies, 1993. Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. *Plant Cell Environ.*, 16: 341–349

Tung, B.T. and N.T. Hai, 2016. Phytochemical and pharmacology effect of *Panax notoginseng*. *J. Appl. Pharm. Sci.*, 6: 174–178

Urban, J., M. Ingwers, M.A. McGuire and R.O. Teskey, 2017. Stomatal conductance increases with rising temperature. *Plant Signal Behav.*, 12: e1356534

Wang, H.Z., L. Han, Y.L. Xu, J.L. Niu and J. Yu, 2016. Characteristics of stomatal conductance of *Populus pruinosa* and the quantitative simulation. *Sci. Silvae Sin.*, 52: 136–142

Wang, Y., X. He and G. Zhou, 2001. Characteristics and quantitative simulation of stomatal conductance of *Aneurolepidium chinense*. *J. Appl. Ecol.*, 12: 517–521

Yu, G., J. Zhuang and Z. Yu, 2001. An attempt to establish a synthetic model of photosynthesis-transpiration based on stomatal behavior for maize and soybean plants grown in field. *J. Plant Physiol.*, 158: 861–874