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Full Length Article

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

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

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

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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 is rarely 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(φ), 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:

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

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

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

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

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

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

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

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

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

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.

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

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

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.

$$g_s = \frac{mA_n h_s}{C_s} + b \quad (12)$$

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 $A_n h_s/Cs$ 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.

$$g_s = \frac{mA_n}{(C_s - \Gamma)(1 + VPD_S / VPD_0)} + g_{s0} \quad (13)$$

Where, m, VPD_0, and g_{s0} are model parameters; Γ 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:

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

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

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

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

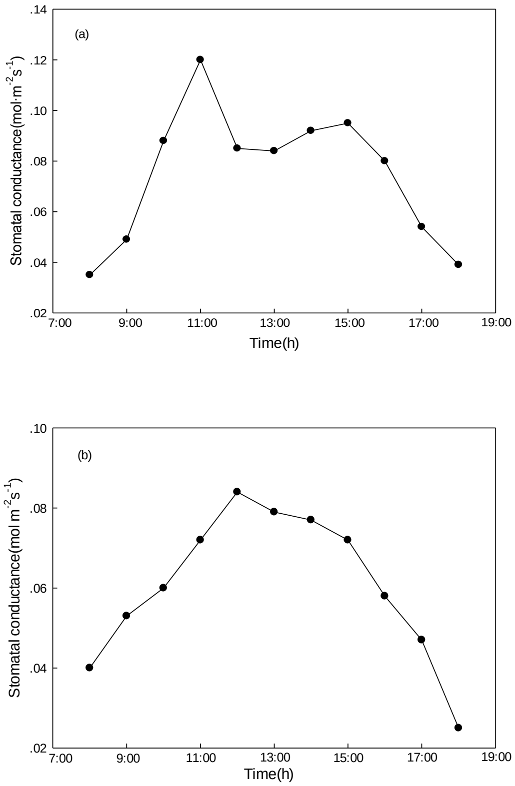

Fig. 1: The diurnal variation of stomatal conductance of *P. notoginseng* leaves on (a) sunny day and (b) cloudy day

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

The gs Model of *P. notoginseng* Leaves

The simulation results of each model are given 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 (Fig. 3).

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 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

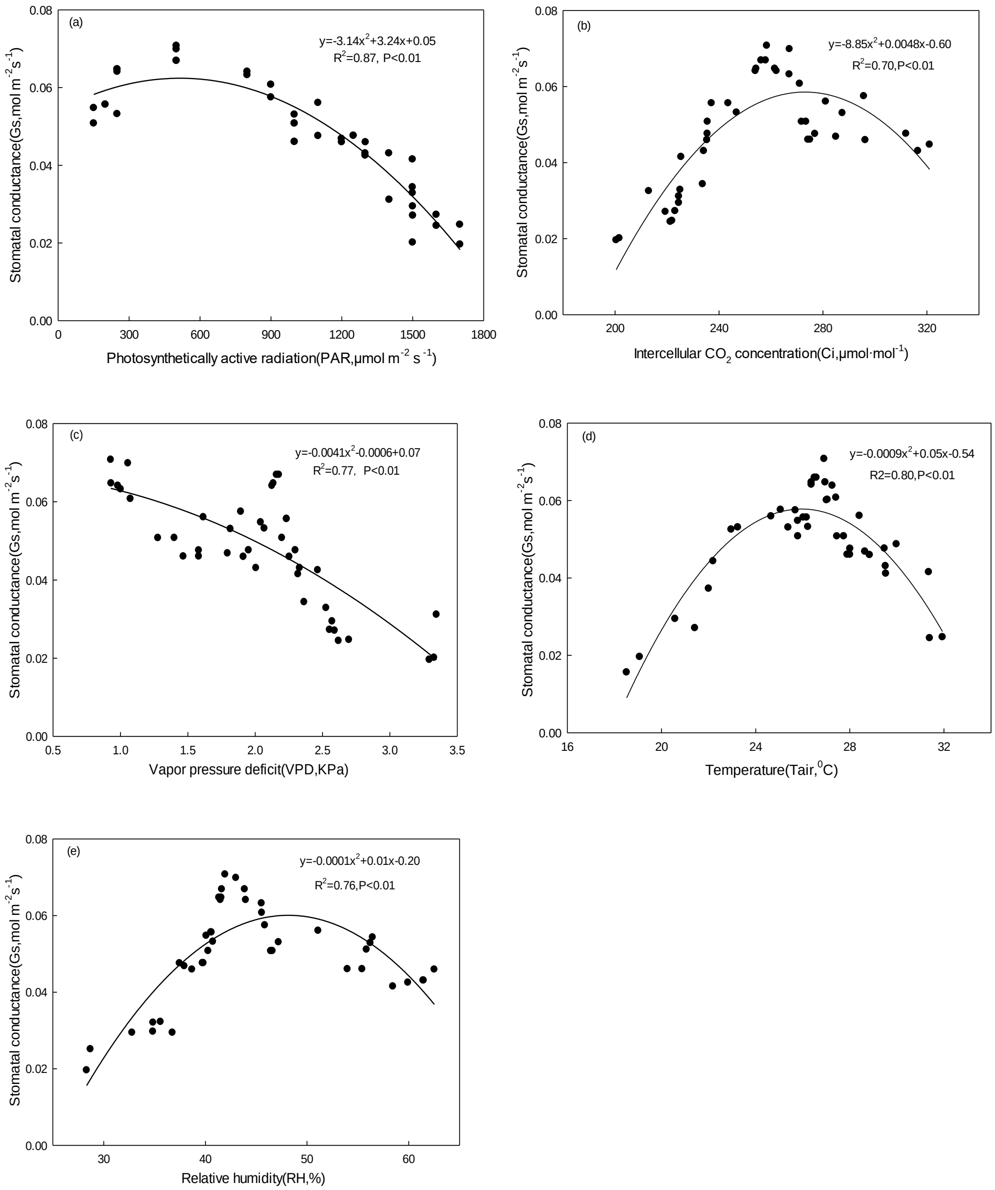

Fig. 2: The relationship between stomatal conductance of *P. notoginseng* leaves and environmental factors

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. 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 prediction effect, the number of parameters is large and no specific biological

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)
	whole day	gs= -0.218-0.077Vpd+0.15T_{air}+0.552PAR	309	128.526	Vpd, T_{air} and PAR	0.775**
Sunny day	morning	gs= -0.076-1.992Vpd+0.933T_{air}+1.183PAR	137	33.378	Vpd, T_{air} and PAR	0.855**
	afternoon	gs=0.012+0.005Ci-1.127Vpd+0.443T_{air}+0.598PAR	172	106.533	Ci, Vpd, T_{air} and PAR	0.810**
	whole day	gs= -0.151-1.512Vpd+0.968T_{air}+0.473PAR	318	63.428	Vpd, T_{air} and PAR	0.786**
Cloudy day	morning	gs= -0.23-2.438RH-6.074Vpd+4.251T_{air}+0.784PAR	135	121.156	RH, Vpd, T_{air} and PAR	0.824**
	afternoon	gs= 0.146+0.379Ci-2.231RH-5.553Vpd+2.989T_{air}+1.208PAR	183	44.804	Ci, RH, Vpd, T_{air} and PAR	0.708**
	whole day	gs= -0.042-1.314Vpd+0.695T_{air}+0.534PAR	627	145.038	Vpd, T_{air} and PAR	0.888**
Total	morning	gs= -0.055-1.365Vpd+0.806T_{air}+0.454PAR	272	46.065	Vpd, T_{air} and PAR	0.778**
	afternoon	gs= -0.196-1.122Vpd+0.970T_{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)
	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**
Jarvis model 1	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**
	whole day	a=144.32,b=-0.567,c=0.003,d=0.003	0.809**
Jarvis model 2	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**
	whole day	m=0.078,b=0.322	0.752**
Ball-Berry model 1	morning	m=0.085,b=0.268	0.698**
	afternoon	m=0.634,b=0.421	0.701**
	whole day	m=6825.31, VPD_0=0.001, and g_{s0}=0.023	0.789**
Ball-Berry model 2	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

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:

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

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.

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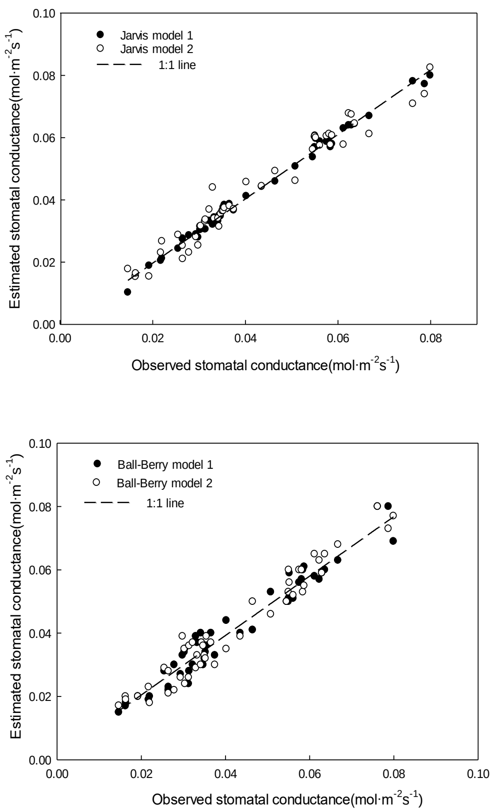

Fig. 3: Comparison of estimated and measured values of stomatal conductance of *P. notoginseng* leaves

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

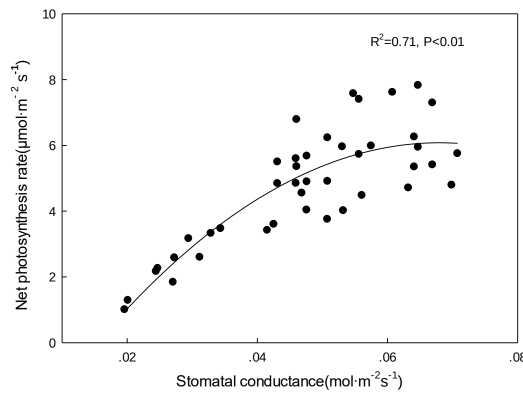

Fig. 4: The relationship between net photosynthesis rate and stomatal conductance

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