

## Environmental Responses and Modeling of Leaf Stomatal Conductance in Apple Trees on the Loess Plateau (Postprint)

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### Abstract

Stomatal conductance ( $g_s$ ) is a crucial parameter for quantifying the exchange rates of water, CO<sub>2</sub>, and other substances between plants and the external environment, and its observation and simulation can effectively indicate the status of material exchange and various physiological parameters. Using the LI-6400 portable photosynthesis system, we observed various physiological parameters of apple tree leaves on the Loess Plateau, analyzed the diurnal variation characteristics of  $g_s$  and its response relationships with environmental factors, and simulated  $g_s$  using the Jarvis model and the Ball-Woodrow-Berry (BWB) model. The results demonstrate: (1) The diurnal variation of  $g_s$  in apple trees on the Loess Plateau exhibited a bimodal curve during observation days in August and September when temperatures were high and radiation was intense. In the morning (8:00–12:00), as solar radiation gradually intensified, stomata opened, and  $g_s$  reached its first peak at 11:00–13:00; at noon (12:00–14:00), due to increased air temperature ( $T_a$ ), stomata closed to prevent excessive water loss from cells, resulting in a brief “midday depression of photosynthesis” phenomenon; in the afternoon (14:00–18:00), as  $T_a$  and photosynthetically active radiation (PAR) decreased,  $g_s$  gradually increased and reached its second peak at 15:00–17:00. (2) Through grey correlation analysis, the correlation degree between  $g_s$  and environmental factors was found to be in the following order: PAR (0.731) > CO<sub>2</sub> concentration ( $C_a$ , 0.712) > vapor pressure deficit (VPD, 0.702) >  $T_a$  (0.689) > relative humidity ( $h_s$ , 0.673). The response relationship between  $g_s$  and environmental factors manifested as:  $g_s$  increased with increasing PAR,  $T_a$ ,  $C_a$ , and  $h_s$ , and decreased with increasing VPD. (3) The simulation results of  $g_s$  indicate that the coefficient of determination (0.678), modified coefficient of efficiency (0.335), and modified coefficient of agreement (0.803) of the Jarvis model were all superior to the corresponding values of the BWB model (0.329, -1.630, 0.138), while the mean absolute error (0.103) was smaller than that of the BWB model (0.143), demonstrating that the Jarvis model provided superior

simulation performance. This analytical study of the environmental response and simulation of  $g_s$  in apple tree leaves on the Loess Plateau holds significant importance for understanding temporal variations in water demand of apple tree leaves throughout the day and for further improving water resource utilization efficiency in apple cultivation in this region.

## Full Text

### Environmental Response and Simulation of Stomatal Conductance in Apple Tree Leaves on the Loess Plateau

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#### Abstract

Stomatal conductance ( $g_s$ ) is a critical parameter that measures the exchange rate of water,  $CO_2$ , and other substances between plants and the external environment. The observation and simulation of  $g_s$  can effectively indicate material exchange processes and various physiological parameters. Using a portable photosynthesis system, we observed the physiological parameters of apple trees on the Loess Plateau, analyzed the diurnal variation characteristics of  $g_s$  and its response relationships with environmental factors, and simulated  $g_s$  using the Jarvis model and the Ball-Woodrow-Berry (BWB) model. The results show that: (1) The diurnal variation of  $g_s$  in apple trees on the Loess Plateau exhibited a bimodal curve during the observation days in August and September when temperatures were high and radiation was strong. In the morning (8:00–12:00), as solar radiation gradually increased, stomata opened and  $g_s$  reached its first peak between 11:00 and 13:00. At midday (12:00–14:00), to avoid excessive water loss from cells as temperature ( $T_a$ ) increased, stomata closed, resulting in a temporary “midday depression of photosynthesis.” In the afternoon (14:00–18:00), as  $T_a$  and photosynthetically active radiation (PAR) decreased,  $g_s$  gradually increased and a second peak appeared between 15:00 and 17:00. (2) Through grey relational degree analysis, the correlation between  $g_s$  and various environmental factors was found to be, in descending order: PAR (0.731) >  $CO_2$  concentration (Ca, 0.712) > vapor pressure deficit (VPD, 0.702) >  $T_a$  (0.689) > relative humidity (hs, 0.673). The response relationships between  $g_s$  and environmental factors showed that  $g_s$  increased with increasing PAR,  $T_a$ , Ca, and hs, but decreased with increasing VPD. (3) The simulation results for  $g_s$  indicated that the Jarvis model performed well, with higher values for the determination coefficient (0.678), modified coefficient of efficiency (0.335), and modified index of agreement (0.803) compared to the BWB model (0.329, -1.630, and 0.138, respectively), while its mean absolute error (0.103) was smaller than

that of the BWB model (0.143). Through systematic analysis of the environmental response and simulation of  $g_s$  in apple tree leaves on the Loess Plateau, this study provides important insights for understanding the temporal changes in water demand by apple tree leaves throughout the day and for improving water use efficiency in apple cultivation in this region.

**Keywords:** stomatal conductance; grey relational degree; apple tree; Loess Plateau

## 1. Study Area Overview

The experimental plot was located at the Dongyang Experimental Research Base of the Institute of Plant Protection, Shanxi Academy of Agricultural Sciences, situated in the central terrain region of Shanxi Province. The area belongs to a temperate monsoon climate zone, with concentrated precipitation in summer and autumn, and relatively dry conditions in winter and spring. The average annual precipitation is 450 mm, the average annual temperature is 9.5 °C, and the average annual wind speed is 2.4 m · s<sup>-1</sup>. The experimental plot contained apple trees with an average crown width of 316 cm × 318 cm and an average ground diameter of 10.9 cm.

### 2.1 Experimental Design and Methods

Observations were conducted during the main growing season of apple trees from June to September. In the experimental plot, three apple trees with good growth conditions were selected as sample trees. A LI-6400 portable photosynthesis system (LI-COR, USA) was used to observe physiological parameters including net photosynthetic rate ( $P_n$ , mol · m<sup>-2</sup> · s<sup>-1</sup>), transpiration rate ( $T_r$ , mmol · m<sup>-2</sup> · s<sup>-1</sup>), intercellular CO<sub>2</sub> concentration ( $C_a$ , mol · mol<sup>-1</sup>), and leaf surface CO<sub>2</sub> concentration ( $C_s$ , mol · mol<sup>-1</sup>). During the observation process, three sun-exposed leaves were selected on each sample tree, and each parameter was recorded repeatedly three times. Observations were made from 8:00 to 18:00 at 2-hour intervals, with adjustments made on different observation dates according to weather conditions and sunrise/sunset times. Additionally, to obtain meteorological parameters such as vapor pressure deficit (VPD), air temperature ( $T_a$ ), relative humidity (hs), and wind speed ( $u$ , m · s<sup>-1</sup>) within the sample plot, a small weather station was set up for observations. After data collection and processing, SPSS 24.0 was used for data preprocessing to facilitate subsequent model simulation.

### 2.2 Introduction to $g_s$ Models

The Jarvis model comprehensively considers the effects of PAR,  $T_a$ , and  $C_a$  on plant leaf  $g_s$ , with the following expression:

$$g_s = g_{smax} \cdot f_1(PAR) \cdot f_2(VPD) \cdot f_3(T_a) \cdot f_4(C_a)$$

where  $f_1(PAR)$ ,  $f_2(VPD)$ ,  $f_3(Ta)$ , and  $f_4(Ca)$  are response functions of  $g_s$  to each environmental factor. In previous studies, scholars have proposed different expressions for the single-factor response models. The commonly used forms are:

$$\begin{aligned} f_1(PAR) &= \frac{a_1 + PAR}{a_2 + PAR} \\ f_2(VPD) &= 1 - a_3 \cdot VPD \\ f_3(Ta) &= a_4 \cdot Ta + a_5 \cdot Ta^2 \\ f_4(Ca) &= 1 - a_6 \cdot Ca \end{aligned}$$

where  $a_1$ ,  $a_2$ ,  $a_3$ ,  $a_4$ ,  $a_5$ , and  $a_6$  are parameters to be determined.

The BWB model assumes a linear relationship between  $g_s$  and net photosynthesis rate ( $A$ ), which largely describes the mechanism of stomatal opening and closing. The calculation formula is:

$$g_s = g_0 + m \cdot \frac{A \cdot hs}{C_s}$$

where  $m$  and  $g_0$  are parameters to be determined;  $A$  is the photosynthetic rate;  $hs$  is relative humidity; and  $C_s$  is leaf surface  $CO_2$  concentration.

### 2.3 Model Simulation Accuracy Evaluation Indicators

By comparing measured leaf stomatal conductance with simulated results from each model, the simulation accuracy of the models can be determined. Following the indicators selected by Legates and McCabe (1999), this study used the determination coefficient ( $R^2$ ), modified coefficient of efficiency ( $E$ ), modified index of agreement ( $d$ ), and mean absolute error (MAE) to evaluate model simulation accuracy:

$$R^2 = \left[ \frac{\sum_{i=1}^N (O_i - \bar{O})(M_i - \bar{M})}{\sqrt{\sum_{i=1}^N (O_i - \bar{O})^2} \sqrt{\sum_{i=1}^N (M_i - \bar{M})^2}} \right]^2$$

$$E = 1 - \frac{\sum_{i=1}^N |O_i - M_i|}{\sum_{i=1}^N |O_i - \bar{O}|}$$

$$d = 1 - \frac{\sum_{i=1}^N |O_i - M_i|}{\sum_{i=1}^N (|M_i - \bar{O}| + |O_i - \bar{O}|)}$$

$$MAE = \frac{1}{N} \sum_{i=1}^N |O_i - M_i|$$

where  $O_i$  is the measured leaf stomatal conductance ( $\text{mol} \cdot \text{H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ );  $M_i$  is the simulated stomatal conductance ( $\text{mol} \cdot \text{H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ );  $\bar{O}$  is the mean measured stomatal conductance ( $\text{mol} \cdot \text{H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ); and  $N$  is the total number of samples. A model is considered to have high simulation accuracy if it has larger  $R^2$ , E, and d values, smaller MAE values, and a slope close to 1.

## 2.4 Grey Relational Degree Analysis

Grey relational degree analysis primarily reflects the degree of association between variables based on the similarity or consistency of their development trends. Before conducting grey relational degree analysis on gs, a grey system must first be established. Using 1-2 typical days with clear weather and good data records as the data source, gs was set as the reference sequence, and the five environmental factors of PAR, Ta, Ca, VPD, and hs were set as comparative sequences to determine the correlation coefficients ( $\xi_i$ ) and relational degrees ( $r_i$ ).

**2.4.1 Dimensionless Processing** Since the environmental factors affecting apple tree leaf gs have different physiological meanings and value ranges, the data require dimensionless standardization. Common dimensionless processing methods include mean normalization, initial value normalization, and range transformation. This study primarily used range transformation for data processing.

**2.4.2 Correlation Coefficients and Relational Degree** Grey relational degree analysis was performed on the dimensionless data to obtain  $\xi_i$  and  $r_i$  between gs and each environmental factor. The correlation degree essentially refers to the similarity of curve trend development. In this study, gs was selected as the reference sequence, and PAR, Ca, VPD, Ta, and hs were selected as comparative sequences to calculate  $\xi_i$  and  $r_i$  between the reference sequence and comparative sequences at each time point (i.e., each point on the curve). The calculation methods are as follows:

$$\xi_{xi}(k) = \frac{\Delta_{min} + \rho \cdot \Delta_{max}}{\Delta_{xi}(k) + \rho \cdot \Delta_{max}}$$

$$r_i = \frac{1}{N} \sum_{k=1}^N \xi_{xi}(k)$$

where  $\rho$  is the resolution coefficient, generally between 0 and 1, typically taken as 0.5;  $\Delta_{min}$  is the minimum difference between the reference sequence and comparative sequences;  $\Delta_{max}$  is the maximum difference;  $\Delta_{xi}(k)$  is the absolute difference between the reference sequence and comparative sequences at each point;  $x_i$  represents the five comparative sequences of PAR, Ca, VPD, Ta, and

hs;  $k$  represents the observation points of environmental factors ( $k = 1, 2, \dots$ ); and  $N$  is the total number of observations for each environmental factor.

### 3.1 Diurnal Variation of Apple Tree $g_s$

Based on measured  $g_s$  data from the main growing season (June–September) of apple trees, clear weather conditions were selected each month to analyze leaf  $g_s$  variation [Figure 1: see original paper]. The results show that the diurnal variation of apple tree leaf  $g_s$  exhibited a bimodal curve on observation days in August and September when temperatures were high and radiation was strong. In the morning, as light intensity continuously increased, stomatal aperture gradually expanded, and  $g_s$  reached its first peak between 11:00 and 13:00. At midday, high temperature and radiation conditions increased the water vapor pressure gradient between the leaf interior and exterior (midday temperature generally around 36.8 °C), and transpiration gradually intensified. To reduce excessive water loss, stomata closed and  $g_s$  decreased. In the afternoon (14:00–18:00), as transpiration rate decreased, leaf water potential recovered to some extent,  $g_s$  gradually increased and exhibited a brief upward trend with a second peak, after which  $g_s$  tended to decline. The afternoon  $g_s$  peak was consistently lower than the morning peak.

#### 3.2.1 Grey Relational Degree Analysis

Based on dimensionless standardized data, the correlation coefficients  $\xi_i$  and relational degrees  $r_i$  between  $g_s$  and each environmental factor were calculated. The results show that the correlation between  $g_s$  and environmental factors was, in descending order: PAR (0.731) > Ca (0.712) > VPD (0.702) > Ta (0.689) > hs (0.673). PAR and Ca showed relatively close relationships with  $g_s$  and had greater influence on stomatal aperture, while hs had the lowest correlation with  $g_s$ .

#### 3.2.2 Response of $g_s$ to Environmental Factors

Sunlight is an important condition for plant photosynthesis and transpiration and a significant factor affecting leaf  $g_s$ . As shown in [Figure 3: see original paper],  $g_s$  gradually increased with increasing PAR. In the morning (8:00–12:00), PAR gradually increased, and  $g_s$  reached its first peak between 11:00 and 13:00. After 12:00–14:00 (midday), PAR continued to strengthen, and when it exceeded  $1200 \text{ W} \cdot \text{m}^{-2}$  (midday PAR generally around  $1385 \text{ W} \cdot \text{m}^{-2}$ ), to reduce excessive water loss, stomata closed and  $g_s$  consequently decreased. In the afternoon (14:00–18:00), as PAR and  $T_r$  decreased, leaf water potential recovered to some extent,  $g_s$  showed a brief upward trend and reached a second peak, after which  $g_s$  tended to decline.

$\text{CO}_2$  is an important raw material for plant photosynthesis. It is generally believed that low Ca can promote stomatal opening, while high Ca causes rapid stomatal closure. The response relationship between  $g_s$  and Ca shows that

when Ca was low, gs gradually increased with increasing Ca; when Ca increased beyond  $375 \text{ mol} \cdot \text{mol}^{-1}$ , gs showed a more obvious decreasing trend with Ca. The Ca range for maintaining relatively high gs was approximately  $350\text{--}375 \text{ mol} \cdot \text{mol}^{-1}$ ; too high or too low Ca would have an inhibitory effect on plant gs.

The response relationship between gs and VPD shows that gs gradually decreased with increasing VPD. Throughout the day, VPD began to continuously increase from 8:00–12:00, with a small decrease in gs; at midday (12:00–14:00), VPD increased significantly, with a peak reaching 3.784 kPa and a maximum of 7.107 kPa. Stomata closed to avoid excessive water loss, and gs values rapidly decreased.

It is generally believed that the effect of Ta on plant leaf gs is that gs tends to increase with rising Ta, but when Ta exceeds a certain limit, gs rapidly decreases. The results show that gs gradually increased with rising Ta, reaching a maximum around  $30\text{--}35\text{ }^{\circ}\text{C}$ , after which gs gradually decreased with further Ta increase.

The response relationship between gs and hs shows that gs increased with increasing hs. Throughout the day, hs was relatively high in the early morning (average about 52.191%), and gs increased with hs; in the afternoon (14:00–18:00), as Ta and VPD increased, hs rapidly decreased, and gs also showed a downward trend due to high temperature effects.

### 3.3.1 Determination of Jarvis and BWB Model Expressions

Based on the single-factor response models for gs in the Jarvis model, different combinations of factor calculation formulas can determine various forms of Jarvis model expressions. This study compared the simulation results of different Jarvis model expressions based on observed apple tree leaf gs data, and determined the optimal model expression by comparing  $R^2$  values. Additionally, SPSS 24.0 was used to fit the observed data and determine the parameter values, ultimately establishing the Jarvis model expressions. The specific results are shown in and .

### 3.3.2 Comparison of gs Model Accuracy

The comparison between measured gs and Jarvis model-simulated gs during the main growing season of apple trees is shown in [Figure 4: see original paper]. The evaluation metrics for model simulation accuracy are presented in . The results show that the simulated gs values for apple trees calculated by the Jarvis model were more concentrated in the scatter plot, with a linear fitting equation slope (0.678) and  $R^2$  (0.335) that were higher than the corresponding values for the BWB model (0.329 and -1.630, respectively). The Jarvis model also showed higher E and d values and lower MAE compared to the BWB model. Therefore, in this study, the Jarvis model demonstrated higher simulation accuracy for apple tree leaf gs.

#### 4. Discussion

The diurnal variation of  $g_s$  reached its first peak between 11:00 and 13:00; at midday, due to increased  $T_a$ , stomata closed under intense transpiration, and  $g_s$  decreased; in the afternoon, as  $T_r$  weakened,  $g_s$  recovered and reached a second peak between 15:00 and 17:00, with the afternoon peak consistently lower than the morning peak.

In the response relationships with environmental factors, leaf  $g_s$  showed an upward trend with increasing PAR,  $C_a$ ,  $h_s$ , and  $T_a$ , but decreased after exceeding certain thresholds for each factor. This conclusion is consistent with the results of Chai Mengying on apple tree leaf  $g_s$  response to PAR, Wang Haizhen et al. on *Populus euphratica*  $g_s$  response to  $C_a$  and  $T_a$ , and Si Jianhua et al. on *Populus pruinosa*  $g_s$  response to  $h_s$ . However, it differs from the results of Ruan Chengjiang et al. on seabuckthorn  $g_s$  response to  $C_a$  in the Loess Hilly Region and Tang Fengde et al. on broadleaved Korean pine forest leaf  $g_s$  response to  $C_a$  and  $h_s$  in Changbai Mountain, which may be related to differences in regional geography and plant species.

Regarding the response of  $g_s$  to VPD, the results show that  $g_s$  decreased with increasing VPD, consistent with the findings of Wang Haizhen et al. on *Populus euphratica* and Zhou Lina et al. on understory ginseng leaf  $g_s$ . The different response relationships between  $g_s$  and environmental factors are due to variations in plant physiological characteristics and environmental adaptation mechanisms.

The LI-6400 portable photosynthesis system was used to observe apple tree  $g_s$  and analyze its diurnal variation characteristics under clear weather conditions. The results show that apple tree  $g_s$  exhibited a bimodal curve on observation days with high temperature and strong radiation in August and September, consistent with the findings of Gao Zhaoquan et al. on apple trees under different water conditions and Li Mingxia et al. on apple trees at the end of the fruiting period. The reason is that in the morning, as PAR,  $T_a$ , and  $C_a$  gradually increased, stomatal aperture expanded, leading to accelerated  $P_n$  and increased  $g_s$ ; when environmental factors exceeded certain thresholds, leaves closed stomata under high temperature and VPD to reduce excessive water loss, causing  $g_s$  to decrease.

#### 5. Conclusions

This study systematically examined apple tree  $g_s$  on the Loess Plateau, first analyzing the diurnal variation characteristics of leaf  $g_s$  and explaining the response relationships between  $g_s$  and environmental factors, then conducting simulation analysis using the Jarvis model. The main conclusions are as follows:

- (1) The diurnal variation of  $g_s$  in apple trees on the Loess Plateau exhibited a bimodal curve on observation days with high temperature and strong radiation in August and September, with the morning peak consistently higher than the afternoon peak. The reasons are: in the morning, in-

fluenced by PAR, stomata opened and  $g_s$  rapidly increased, reaching its first peak between 11:00 and 13:00; at midday, as  $T_a$  increased, stomata closed under intense transpiration and  $g_s$  decreased; in the afternoon, as  $T_r$  weakened,  $g_s$  recovered and reached a second peak between 15:00 and 17:00, with the afternoon peak consistently lower than the morning peak.

- (2) The correlation between  $g_s$  and environmental factors was, in descending order:  $PAR > Ca > VPD > T_a > h_s$ . The response relationships showed that  $g_s$  increased with increasing PAR,  $T_a$ , Ca, and  $h_s$ , but decreased with increasing VPD. The different response relationships are due to: throughout the day, as PAR,  $T_a$ , and Ca gradually increased, stomatal aperture expanded, accelerating Pn and increasing  $g_s$ ; when environmental factors exceeded certain thresholds, leaves closed stomata under high temperature and VPD stimulation to reduce excessive water loss, causing  $g_s$  to decrease. Higher  $h_s$  values corresponded to early morning, evening, or cloudy conditions with weak light, where  $g_s$  values were lower compared to clear weather conditions.
- (3) The simulation results for  $g_s$  showed that the Jarvis model had good simulation performance. In the future, simulation studies of  $g_s$  for various crops under arid and semi-arid climate conditions, as well as estimation and simulation of evapotranspiration and ecological water requirements for natural vegetation in arid regions, should be strengthened to further explore the applicability of the Jarvis model.

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