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几个气孔模型在自然条件下的适用性

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摘要: 在自然条件下,用气孔下腔与叶面间的水汽压差(VPD_s)取代原有气孔模型中的大气湿度因子,可以明显提高气孔模型在自然条件下的适用性。理论分析指出,在气孔模型中,用 VPD_s 表达气孔导度对湿度的响应与用蒸腾速率表达气孔导度对蒸腾失水的响应是等价的。

关键词: 气孔导度;模型

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Applicability of Some Stomatal Models to Natural Conditions*

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Abstract: Under natural conditions, the use of vapor pressure deficit between mesophyll cell surface and ambient air (VPD_s) instead of atmospheric humidity factors in some stomatal models may markedly promote the applicability of stomatal models. It has been pointed out from theoretical analysis that the expression of the responses of stomatal conductance to VPD_s is equivalent to the expression of responses of stomatal conductance to water loss of transpiration in stomatal models.

Key words: stomatal conductance; model

The stomatal models used as submodels in many ecological models are mainly semi-empirical, among which the one proposed by Ball *et al*.[1] is widely accepted[2-5]. These stomatal models have been constructed based on the data obtained under laboratory conditions. Under natural conditions, however, the feedback reactions among the interactions between physiological and physical processes are different. For example, an increase in solar radiation will induce an increase in leaf temperature and photosynthesis. But leaf temperature is controlled artificially under laboratory condition, and therefore may be different to an extent from air temperature which is dependent on solar radiation. The validity of stomatal models under natural conditions is often taken for granted and seldom examined critically. The objective of this study is to make a theoretical analysis of several stomatal models based on the one of Ball-Woodrow-Berry, and to evaluate the models by fitting with experimental data of an entire growth period under natural field conditions. The fine stomatal models studied are as follows:

(1) Ball *et al*.[1] constructed the following mathematical relation between stomatal conductance and environmental and physiological factors.

$$g_s = a_1 \frac{A_n h_s}{C_s} + g_o \qquad (1)$$

in which g_s and A_n are stomatal conductance and photosynthetic rate respectively. h_s and C_s are relative humidity and CO_2 concentration over the leaf surface respectively, and a_1 and g_o are parameters. It will be referred to as BWB model.

(2) Leuning[6] revised the BWB model by replacing relative humidity (h_s) with air water vapor deficit (VPD_a) and also C_s with C_s-Γ and formulated as follows:

$$g_s = a_1 \frac{A_n}{(C_s - \Gamma)(1 + VPD_a/VPD_o)} + g_o \qquad (2)$$

in which Γ is the CO_2 compensation point.

(3) Yu and Wang gave a more realistic model by replacing VPD_a for VPD_s[7,8].

$$g_s = a_1 \frac{A_n}{(C_s - \Gamma)(1 + VPD_s/VPD_o)} + g_o \qquad (3)$$

(4) Monteith[9] basing on many experimental results proposed that stomata respond to humidity in a way that stomatal conductance decreases linearly with an increase

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in the rate of transpiration (E) .

$$g_s / g_{sm} = 1 - E / E_m \qquad (4)$$

in which , g_{sm} and E_m are characteristic parameters for stomatal conductance and transpiration.

Dewar[10] combined Eq 4 with BWB model , and obtained :

$$g_s = \frac{a_1 A_n}{C_s - \Gamma}(1 - E / E_m) + g_o \qquad (5)$$

the parameter g_o is always a small value approaching zero.

1 Materials and Method

Experiments were conducted at Yucheng Comprehensive Experimental Station (36°57′N, 116°36′E, 20 m above sea level). The rates of photosynthesis and transpiration, and stomatal conductance of winter wheat (*Triticum aestivum* L.) leaves are measured from tillering stage to maturity (March 29 - June 3, 1998). Clear or cloudy days were selected for observing leaf photosynthesis and other physiological traits and corresponding environmental factors. Observations were made on a total of 32 days. Measurements were performed every 2 hours from 8:00 to 18:00 on each observation day. Three plants were selected and leaves of the upper, middle and lower layers of each plant were used for measurements. When intercelular CO_2 (C_i) was less than 100 $\mu mol \cdot mol^{-1}$, the data set was excluded as it was considered to be unreasonable. The infrared CO_2 analysis system CI-301PS of CID Co, USA, was used. The system was calibrated weekly, and has shown its stability. There was ample water and fertilizer supply.

2 Result

To fit Eqs. 1, 2 and 3 with experimental data, parameters reflecting the physiological characters in the equations, VPD_o and Γ, should be given in advance. The CO_2 concentration point was assumed to be about 50 $\mu mol \cdot mol^{-1}$, and VPD_o was adjusted so that the relation between stomatal conductance and stomatal conductance index (algebraic formula on the right of equations including environmental and physiological elements) achieved the highest coefficient of correlation which was taken as the best fit that was obtained.

The coefficient of correlation obtained between stomatal conductance and stomatal conductance index was 0.57 ($n = 969$) for the simulation of BWB model (Eq. 1) as shown in Fig. 1. The scattering of points was great, and the precision of simulation was low. Leuning's revised model (Eq. 2), in which the response of stomatal conductance its calculated by replacing the relative humidity with VPD, and it has given a slightly better fitting than BWB model, with a correlation coefficient of 0.59 (Fig. 2). This may be explained that as stomata respond to water loss, there is a closed relation between rate of water loss and vapor pressure deficit than that between water loss and leaf surface humidity[11,12]. Eq. 3 gave a much better simulation with a correlation coefficient of 0.68. There was an considerable improvement of the goodness of fit as shown in Fig. 3. In gaseous diffusion equation proposed by Aphalo and Jarvis[13], stomatal conductance is dependent on vapor pressure deficit between stomatal pore to ambient air more than that in air. Under natural conditions, when the difference in temperature between leaf and air is considerable, the corresponding difference between VPD from stomata to air and that in air should also not be neglected. Influence of the driving force of water loss through transpiration on stomatal conductance must also be considered. As the elemetns of developmental stage and leaf age are included in Fig. 3, there is still scattering of points, although the general trend of points is acceptable.

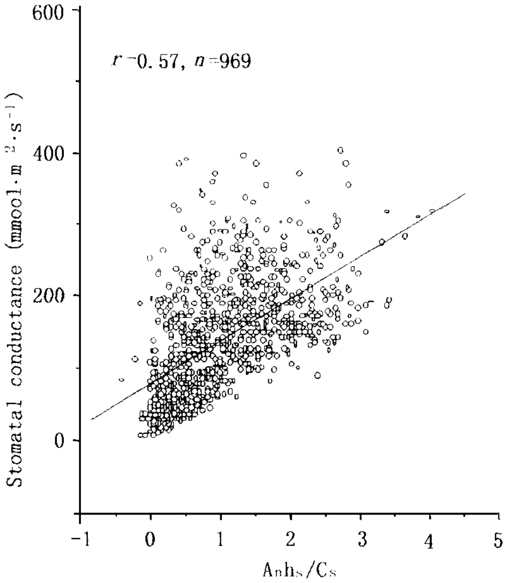

图 1. Ball-Berry 模型中气孔导度指数与气孔导度的测定值的相关关系。

Fig. 1. Relation between observed stomatal conductance and stomatal conductance index in BWB model.

Mott and Parkhurst[14] pointed out that stomatal aperture, which determines stomatal conductance, is more closely related to transpiration, i.e. the rate of water loss, than vapor pressure deficit. So Eq. 4 gives directly the relation between stomatal conductance and transpiration. Using a combined photosynthesis-transpiration-stomatal conductance model in which stomatal conductance was a hyperbolic function of VPD_s, Yu and Wang simulated that stomatal conductance declined linearly with transpiration under changing air humidity[7]. This result suggests an implicit relation between Eqs. 3 and 5. This relation is expounded as follows:

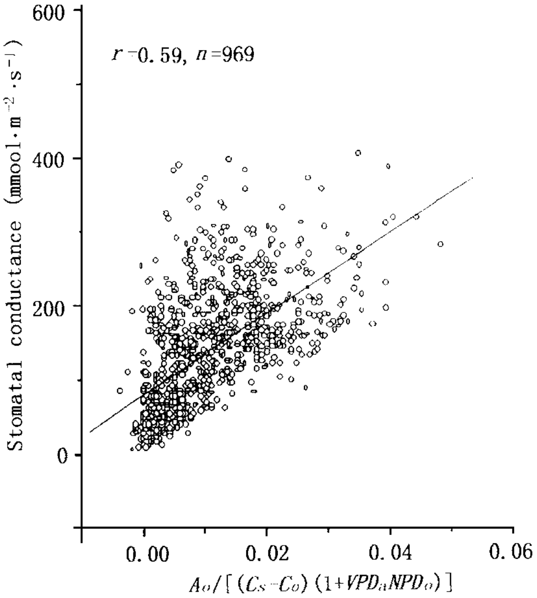

图 2. Leuning **模型气孔导度指数与气孔导度的测定值的相关关系。**

Fig. 2. Relation between observed stomatal conductance and stomatal conductance index in Leuning's revised model.

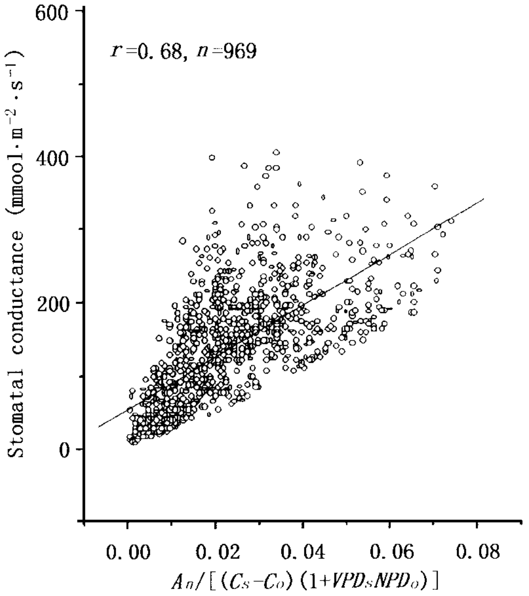

图 3. 公式 3 **中的气孔导度指数与气孔导度的测定值的相关关系。**

Fig. 3. Relation between observed stomatal conductance and stomatal conductance index in Eq. 3.

$$E = g_s VPD_s \tag{6}$$

substitute Eq. 6 to Eq. 4, we obtain

$$g_s / g_{sm} = 1 - VPD_s g_s / E_m \tag{7}$$

After rearrangement it becomes:

$$g_s = \frac{1}{1/g_{sm} + VPD_s / E_m} \tag{8}$$

Taking $VPD_o = E_m / g_{sm}$, it can be expressed as:

$$g_s = g_{sm} \frac{1}{1 + VPD_s / VPD_o} \tag{9}$$

It has been shown that the relation between stomatal conductance and transpiration in Eq. 4 accords with that between g_s and VPD_s theoretically, which means that a linear relation between stomatal conductance and transpiration proposed by Monteith is equivalent to a hyperbolic relation between stomatal conductance and VPD_s as shown in Eq. 3.

3 Conclusions

(1) Under natural conditions, the revised BWB model proposed by Leuning (Eq. 2) may give a slightly higher precision of simulation than does the BWB model. The model in which VPD_a being replaced for VPD_s (Eq. 3) is an augmentation to Leuning model. Under laboratory condition, the difference between leaf and air temperatures can be so small that it will not cause any significant error when VPD values are calculated from saturated vapor at air temperature instead of at leaf temperature, so the two equations are equivalent to each other. However, there is often a significant difference between leaf and air temperatures under natural conditions when the wind speed is low. The modified model (Eq. 3) may greatly improve the precision of simulation.

(2) The model which uses the vapor pressure deficit from stomata to ambient air (VPD_s) to express stomatal responses to humidity is equivalent to that which expresses stomatal responses to transpiration. Under natural conditions, VPD_s is a physical variable, so the application of the augmented model (Eq. 3) is more reasonable.

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