Simulation of the stomatal conductance of winter wheat in response to light, temperature and CO_2 changes

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Abstract

Stoma is a key channel of the water cycle in ecosystems, which is constrained by both physiological and environmental elements. Light and CO_2 responses of stomatal conductance and photosynthesis of winter wheat in the North China Plain were investigated under field conditions. The photosynthetic photon flux density and CO_2 concentration ranged from 0 to 2000 μmol m^{-1} s^{-1} and from 0 to 1400 μmol mol^{-1} respectively.

Stomatal conductance was parameterized by extending an empirical model (Jarvis, 1976) and a revised BWB model (Ball *et al*., 1987; Yu *et al*., 2001). By using hyperbolic equations of photosynthetic responses to light and CO_2 (Thornley 1976), the number of parameters in the model was reduced. The model was validated with data from a light, temperature and CO_2 response experiment. These response curves were observed diurnally with large variations of temperature and vapor pressure deficit. The model interpreted stomatal response under wide variations of environmental factors.

Most of the model parameters, such as initial photon efficiency and maximum photosynthetic rate ($P_{\max}$), have physiological meanings. The model can be expanded to include influences of other physiological elements, e.g. leaf aging and nutrient conditions, and nutrition level, especially leaf nitrogen content.

Key words: stomatal conductance, light intensity, temperature, humidity, CO_2, model

Introduction

Leaf stomata control plant CO_2 absorption through photosynthesis and water loss through transpiration. Their aperture regulates water use efficiency of crops and energy partitioning into sensible and latent heat. Therefore, parameterization of stomatal conductance is essential in the simulation of crop productivity and water using efficiency in agricultural ecosystems. As stomatal aperture is a balance between CO_2 assimilation and water loss, its conductance is related to photosynthesis and transpiration (Cowan, 1965). Stomatal opening affects photosynthesis by regulating intercellular CO_2 concentration, and thereby the biochemical processes in chloroplasts (Yu *et al*., 2001). The extent of stomatal opening is jointly determined by light intensity and water balance of the guard cells. Light intensity affects photosynthesis rate through light receptors to drive CO_2 fixation which lowers intercellular CO_2 concentration, and the guard cells are conditioned jointly by the water balance of bulk leaf tissue and particularly and the CO_2 concentration in the substomatal cavity.

In the simulation of stomatal conductance, the Jarvis (1976) model has been applied widely to the studies of evapotranspiration, land surface processes, and the biogeochemical cycle (e.g., McMurtrie, 1992; Hanan and Prince, 1997; Cox *et al*., 1998). The model is a typical empirical one, which is characterized by multiplying by a series of correction coefficients each representing a factor. It does not include physiological feedbacks from changes in rates of photosynthesis and transpiration due to stomatal movements. A semi-empirical model, the Ball-Berry model (Ball *et al*., 1987), has a solid experimental basis with a linear relation between photosynthesis and stomatal conductance. But to take amount of the feedback interaction between photosynthetic rate and stomatal conductance requires iteration of calculations. In this study, a hybrid stomatal model is proposed, based partly on those empirical and semi-empirical models, which gives a direct calculation of stomatal conductance from solar radiation, temperature, humidity, CO_2 concentration of air and soil water potential, but has physiological relations similar to the Ball-Berry model.

The objective of this study is to construct a Jarvis-type stomatal model with physiological relationships based on Ball-Berry model, so as to enable the model to calculate the conductance directly from environmental variables, while it has a relevant physiological basis.

Method

Experiments were conducted at Yucheng Comprehesive Experiment Station (36°57′N, 116°36′E, 28 m a.s.l.), Chinese Academy of Sciences, which is located in the North China Plain. The light and CO_2 responses of photosynthesis, transpiration, and stomatal conductance of winter wheat were measured in the field. The light and CO_2 response curves were measured in a leaf chamber. Each measurement was made in a short period. Flag leaves were used for measurements, which were conducted at bearing stage (from April 16 to May 6, 2003). Measurement were conducted every 2 h in a day to get the light and CO_2 response curves under natural variation of temperature and humidity by varying light (400-700 nm) intensity between 0 and 2000 μmol m^{-2} s^{-1}, and CO_2 concentrations between 0 and 1400 μmol mol^{-1}. Therefore, environmental conditions varied greatly in light, temperature, and CO_2 concentration.

The infrared CO_2 analysis system LI-COR 6400 (LI-COR Inc., Lincoln) was used. The system was calibrated, and found to give stable performance. The wheat fields were irrigated routinely, according to soil water content and well fertilized. Irrigation water of about 70-100 mm was applied 3 times after the turning-green stage. The area of cultivation was more than 20 ha. For a detailed description of management and natural conditions, see Yu *et al.* (2002).

The model

There are five main environmental factors affecting stomatal conductance under natural conditions, i.e., solar radiation, air temperature, humidity, CO_2 concentration, and soil water potential. The actual stomatal conductance (g_s) can be obtained from the maximum conductance (g_{max}) under suitable conditions modified by correction coefficients for all the above factors (Jarvis, 1976):

$$g_{\mathrm{s}} = g_{\max} f(I) f(T_{\mathrm{a}}) f(C_{\mathrm{a}}) f(D) f(\psi) \qquad (1)$$

in which I is absorbed photosynthetic photon flux density (*PPFD*), T_a is air temperature, C_a is CO_2 concentration, D is vapor pressure deficit and ψ is soil water potential.

Ball *et al.* (1987) proposed a semi-empirical stomatal model in which the mathematical relation between relative humidity at the leaf surface (h_s), CO_2 concentration (C_s) and photosynthetic rate (A_n) was represented by the following equation under conditions of ample water supply:

$$g_{\mathrm{s}} = \mathrm{a}\frac{A_{\mathrm{n}} h_{\mathrm{s}}}{C_{\mathrm{s}}} + \mathrm{g}_0 \qquad (2)$$

in which a is a constant, h_s is the relative humidity and C_s is the CO_2 concentration of air at the leaf surface, g_s is stomatal conductance, and g_0 is a parameter. Since it is the vapor pressure deficit from stomatal pore to leaf surface (D_s) which drives transpiration, D_s should replace h_s in the Ball-Berry model (Leuning, 1995). Here, the D in air is used instead of D_s, because D is a meteorological variable and can be easily obtained. Equation 2 is rewritten as

$$g_s = a\frac{A_n}{(C_s - \Gamma)(1 + D/D_0)} + g_0 \tag{3}$$

in which Γ is the CO_2 compensation point, and D_0 is a parameter reflecting characteristics of response of stomata to atmospheric D (Pa), which determines curvature of humidity response curve of stomatal conductance.

As stomatal conductance begins to increase immediately with increasing light, even below the light compensation point, Yu *et al.* (2001) proposed gross assimilation rate should be used instead of net assimilation, and correspondingly, C_s-Γ should be replaced by C_s in Eq. 3:

$$g_s = a\frac{A_g}{C_s(1 + D/D_0)} \tag{4}$$

where A_g is the gross assimilation rate, and C_s is CO_2 concentration at leaf surface. In this expression, parameter g_0 in Eq. 3 is taken as 0, because A_g and g_s go to 0 in the dark.

A_g is a function of environmental variables. We adopted a revision to take account of the limitation of photosynthesis by stomatal conductance:

$$A_g = \frac{A_m \alpha I \eta C_a}{A_m \alpha I + A_m \eta C_a + \alpha I \eta C_a}\frac{g_s}{g_s + g_{int}} \tag{5}$$

in which, A_m is the maximum catalytic capacity of Rubisco per unit leaf area, α is initial photochemical efficiency, and η is the initial slope of the CO_2 response curve (μmol m^{-2} s^{-1}/μmol mol^{-1}). g_{int} is a parameter. If $g_{int} \rightarrow 0$, $g_s/(g_s + g_{int}) = 1$, the equation shortens to the original light and CO_2 response curve.

A_m is a function of temperature with a maximum given by (Collatz *et al.*, 1991):

$$A_m = A_0 \frac{Q_{10}^{(T_a-25)/10}}{1 + \exp\{[-a_1 + b_1(T_a + 273)]/[R(T_a + 273)]\}} \tag{6}$$

in which a_1, b_1 are parameters, and $A_m = A_0$ at $T_a = 25$ °C and R is the universal gas constant.

It is assumed that $g_s/(g_s + g_{int})$ is determined chiefly by leaf or soil water status for a particular plant. Therefore, Eq. 5 can be converted into the following types

$$A_g = \frac{A_m \alpha I \eta C_a}{A_m \alpha I + A_m \eta C_a + \alpha I \eta C_a} f(\psi) \tag{7}$$

The water-stress coefficient, $f(\psi)$, is simply characterized by a linear relation from the water potential at wilting point (ψ_0) to water potential at field capacity (ψ_m), *i.e.*, relative extractable water (Lagergren and Lindroth, 2002). Therefore, by combining Eqs. 4 and 7, stomatal conductance can be expressed as a function of environmental variables in the following form:

$$g_s = a \frac{A_m \alpha I \eta}{(A_m \alpha I + A_m \eta C_a + \alpha I \eta C_a)} \frac{1}{(1 + D/D_0)} \frac{\psi - \psi_0}{(\psi_m - \psi_0)} \tag{8}$$

Stomata close in the dark, *i.e.*, g_s is zero when I is zero, which is satisfied by Eq. 8. Boundary conditions of stomatal response to light, D and water potential are also satisfied by Eq. 8. The unit of a is the same as that of CO_2 concentration.

In conclusion, the stomatal conductance model (Eq. 8) is based on both the relationship between stomatal conductance and gross photosynthesis (Eq. 4, Yu *et al.*, 2002) and that between photosynthesis and I (Eq. 7, Thornley, 1976). The parameters

α and A_m are related to biochemical processes, which are influenced by environmental factors. The model consists of two parts: (1) the relationship between stomatal conductance and photosynthesis (Eq. 4), where the influences of light, temperature and CO_2 concentration on photosynthesis (Eqs. 6 and 7) and thereby on stomatal conductance are integrated into one expression; and (2) the effects of evaporation demand (D) and soil water potential on stomatal conductance are included in this expression (Eq. 8).

Results

1. Relation between stomatal conductance and photosynthetic rate in the model

Figure 1 demonstrates the responses of stomatal conductance, and net and gross photosynthetic rates to changes in light intensities. It is shown that both stomatal conductance and gross photosynthetic rate start from zero, which is a boundary condition of Eq. 8. But net photosynthetic rate start from a negative value of dark respiration ($-R_d$), the value of which depends on air temperature and other variables. Therefore, the revised version of the Ball-Berry stomatal model (Eq. 4), expressing the relation between g_s and A_g, instead of net assimilation, will give a stronger relation between stomatal conductance and photosynthesis.

To fit Eqs. 2 and 4 with experimental data, parameters reflecting the physiological characters in the equations, D_0 and Γ, should be given in advance. The CO_2 concentration point is assumed to be about 50 μmol mol^{-1}, and D_0 is adjusted so that the relation between stomatal conductance and stomatal conductance index (algebraic formula on the right of equations including environmental and physiological elements) achieves the highest coefficient of correlation which is taken as the best fit is obtained.

The relationship between stomatal conductance and stomatal conductance index in Eq. 2 is significant ($r^2=0.83^{**}$, n=210) for the simulation of original Ball-Berry model in Fig 2a. Eq. 4 gives a much better correlation in Fig. 2b ($r^2=0.91^{**}$, n=210). There is an considerable improvement of goodness of fit. It is because that stomata respond to water loss, the relation between rate of water loss and vapor pressure deficit is closer than that between water loss and leaf surface humidity (Sheriff, 1984; Aphalo and Jarvis ,1991).

2. The dependence of photosynthetic rate on light and CO_2

Naturally, solar radiation on the Plateau is much higher than that in the Plain with a humid climate, where the *I* rarely exceeds 1500 μmol $m^{-2}s^{-1}$. Light response curves of photosynthesis were fitted to data collected from leaves under changing light intensities when other factors were kept stable for each measurement. Figure 3 (a and b) shows two typical light response curves of photosynthesis of wheat in which the photosynthetic rate was observed under different atmospheric conditions of temperature, humidity and CO_2 partial pressure. All light curves are similar in shape, but have different parameters due to differences on temperature and humidity. Temperature ranged from 25 to 30°C in the period of observation, and relative humidity changed from 10% to 50%.

Figure 3 (c, d) shows the CO_2 response of photosynthesis to CO_2 concentration in the range from 0 to 1400 μ mol mol^{-1}. The scatter of points is wider than that of the light response. When photosynthetic rates and light intensity in the field are fitted by a rectangular hyperbola (Fig. 3), a good relation is obtained. The initial slope of the fitted curve (α) is about 0.07 μmolCO$_2$ μmol^{-1}. For common crops, α is lower than its theoretical maximum (0.08), ranging from 0.04 to 0.07 under field conditions (Xu, 1984). The maximum photosynthetic rate is about 30.0 μmol m^{-2}s^{-1}, which is basically the photosynthetic rate at the saturation point of light (Fig. 3). The maximum photosynthetic rate under field conditions varied between 25.0 and 35.0 μmol m^{-2}s^{-1}, and stomatal conductance between 0.2 and 0.4 mol m^{-2}s^{-1}, whereas photosynthetic rate is higher and stomatal conductance lower under CO$_2$ enrichment.

3. Model validation

The data used in model validation are shown light and CO$_2$ responses (Figs. 4 and 5). The response curve of photosynthetic rate to light intensity is a typical Michaelis-Menten curve (Fig. 4). Stomatal conductance corresponds to photosynthesis well in a changing light environment.

Increased atmospheric CO$_2$ concentration will raise the intercellular CO$_2$, and thereby photosynthetic rate. Stomatal conductance decreases with increased CO$_2$ concentration, whereas photosynthetic rate increases (Fig. 5).

As the experiment was conducted under ample water supply, the influence of water stress in Eq. 8 is not included in the validation. The model was run with observational data of meteorological variables as inputs. After maximum carboxylation rate was obtained, the value of other parameters were adjusted according to previous studies (Collatz *et al.*, 1991; Leuning, 1995; Yu *et al.*, 2002), so that there is a very high coefficient of correlations between stomatal conductance and the index of stomatal conductance, *i.e.*, $\frac{A_{\mathrm{m}}\alpha I\eta}{A_{\mathrm{m}}\alpha I + A_{\mathrm{m}}\eta C_{\mathrm{a}} + \alpha I\eta C_{\mathrm{a}}}\frac{1}{1+D/\mathrm{D}_0}$. Then, the measured stomatal conductance was compared with the index. The parameters used were as follows: A_{m} ＝60.0 μmol $\mathrm{m}^{-2}\mathrm{s}^{-1}$, Q_{10}=2.4, a_1=220.0 kJ/mol, b_1=703.0 J mol^{-1} K^{-1}, D_0=3.5 kPa, α=0.06, η=0.03. The constant R is 8.314 J mol^{-1} K^{-1}.

Figures 6 and 7 are comparisons between measured stomatal conductance and the stomatal conductance index under changing light intensities and CO_2 concentrations, respectively. Figure 6 shows that stomatal conductance agrees well with the index calculated from light, temperature, D and CO_2 concentration (Fig. 6). A good linear relationship between stomatal conductance and the index, with a slope of 1.067, and the intercept on the Y-axis of simulated values is -0.01 which is very close to 0. That means the model predicts stomatal conductance quite well. Agreement between measured stomatal conductance and predicted index under changing CO_2 concentration is also good, with the intercept is also near 0, only the spread of points is slightly greater than that of light response (Fig. 7).

Discussion

Plant transpiration is a physical process in which part of the net radiation energy is converted into latent heat under physiological control by changes in stomatal aperture (Jarvis and McNaughton, 1986). In the Penman-Monteith evapotranspiration model based on energy balance, canopy resistance to water vapor diffusion is the sole factor reflecting under physiological regulation (Thom, 1975). Therefore, determination of resistance, the reciprocal of conductance, is a key topic in the simulation of evapotranspiration. In this study, we proposed a stomatal model as a function of solar radiation, CO_2 concentration, and temperature, as well as D and soil water content. The mechanism of stomatal closure remains to be explored under changing climate, which is essential for the evaluation of primary production and water consumption. If it is not necessary to calculate photosynthesis as in some hydrological models (Hatton, 1992; Gottschalck *et al*., 2001), the stomatal model can be directly applied to calculate evapotranspiration.

Besides many relations between stomatal conductance and atmospheric humidity or D_s, Monteith (1995), basing on many experimental results, proposed that stomata respond to humidity in such a way that stomatal conductance decreases linearly with an increase in the rate of transpiration. This linear relationship between stomatal conductance and transpiration is identical to non-linear relationship between the conductance and D_s (Leuning, 1995). Dewar (1995) gave thorough interpretations of stomatal conductance in relation to environmental factors, photosynthesis and transpiration in these stomatal models.

Parameters in empirical models do not have clear physiological significance, which change with the specific plot or variety (Calvet, 2000), and complexity of the determination of their values increases sharply with the number of parameters. Application of the Jarvis model (Eq. 1) usually includes some of the five environmental variables i.e., light intensity, temperature, humidity, CO_2 concentration and soil water. Semi-empirical models are based on physiological characteristics of plant, although they are not theoretical expressions. Parameters used in semi-empirical models with some physiological basis may extend the generality of the model. For example, $P_{\max}$, α, and η have physiological significance, which makes their values meaningful. Some parameters in the model may include the influence of other factors. For example, maximum photosynthetic rate is a function of leaf nitrogen content. As photosynthetic parameters are applied, the relation between stomatal conductance and photosynthetic rate is included, and plant nutrition can be included in the parameter $P_{\max}$.

There are many parameters in empirical stomatal models. The semi-empirical model can reduce the number of parameters by means of theoretical analysis. For example, stomatal conductance and gross photosynthetic rate increase from zero, and this boundary condition suggests a constant ratio of the two quantities and the intercept, g_0 goes to zero (Eq. 4). The introduction of a light and CO_2 response equation (Thornley, 1976) also reduces the number of parameters required when the effects of light and CO_2 are considered separately. Cannell and Thornley (1998) proposed that temperature and CO_2 were two important factors affecting P_n in the form of non-rectangular hyperbolas. In this study, the simple rectangular hyperbola was used as the light response curve.

The model was validated by measurement data under controlled conditions of light and CO_2 over a wide range, designed to verify its universality. The stomatal conductance model was validated by data with a wide range of temperature, including diurnal variation, as well as light intensities and CO_2 concentration.

The climate in the North China Plain is characterized by high solar radiation and low humidity. The light response curve is no longer a hyperbola when the observation time extends, as photosynthetic rate decreases with the increase in light intensity beyond certain limit (Yu *et al*., 2002). In this study, the data were confined to a period from early morning to 11:00 am each day. There is a significant decrease in photosynthetic rate with increasing light intensity after that hour due to photoinhibition, similar to the phenomenon reviewed by Leverenz (1994).

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List of figure captions

Fig. 1 Demonstration of relationship between of stomatal conductance and net and gross photosynthetic rates to changes in light intensities

Fig. 2 Simulation of stomatal conductance by original Ball-Berry model and its revised form, Eq. 4 (Yucheng, 16, 18 April, 2003 **significance level<0.01)

Fig. 3 Fitting the responses of photosynthesis to changes in light intensities and CO_2 concentrations (Yucheng, 16, 21 April and 2, 6 May, 2003)

Fig. 4 Responses of photosynthesis and stomatal conductance to changes in light intensities (Yucheng, 16, 20, 21 April, 2003)

Fig. 5 Responses of photosynthesis and stomatal conductance to changes in CO_2 concentrations (Yucheng, 24, April and 6 May, 2003)

Fig. 6 Stomatal conductance versus stomatal conductance index under changing light intensities (data from Fig. 4)

Fig. 7 Stomatal conductance versus stomatal conductance index under changing CO_2 concentrations (data from Fig. 5)

Fig. 1

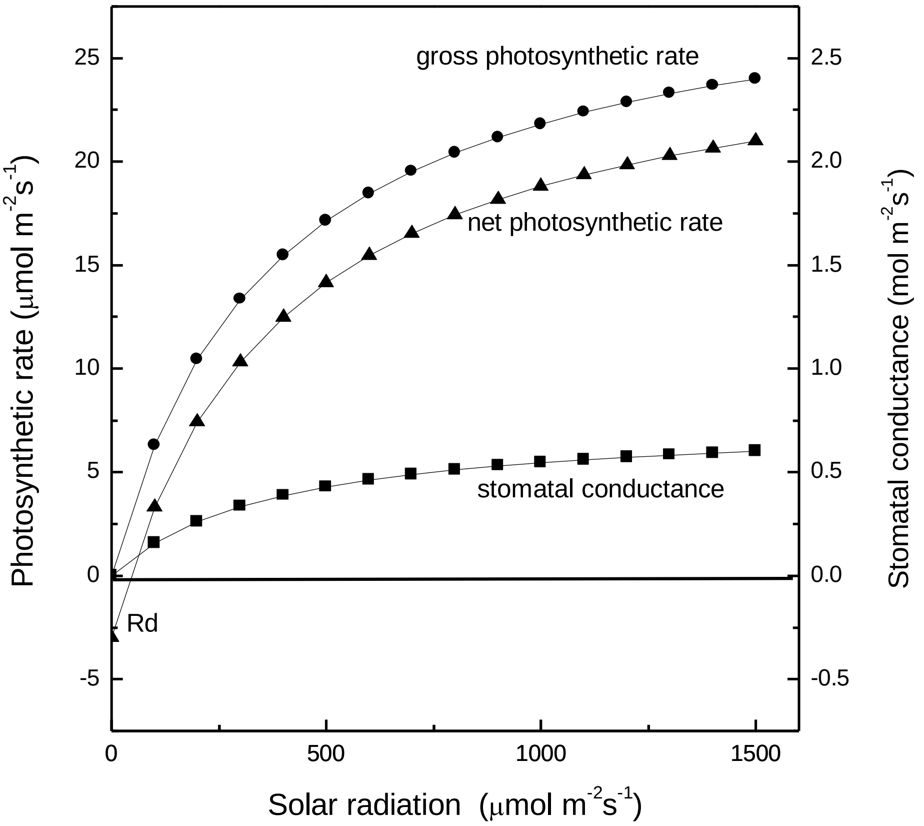

gross photosynthetic rate
net photosynthetic rate
stomatal conductance
Rd
Photosynthetic rate (μmol m-2s-1)
Stomatal conductance (mol m-2s-1)
Solar radiation (μmol m-2s-1)
25
20
15
10
5
0
-5
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
0
500
1000
1500

Fig. 2

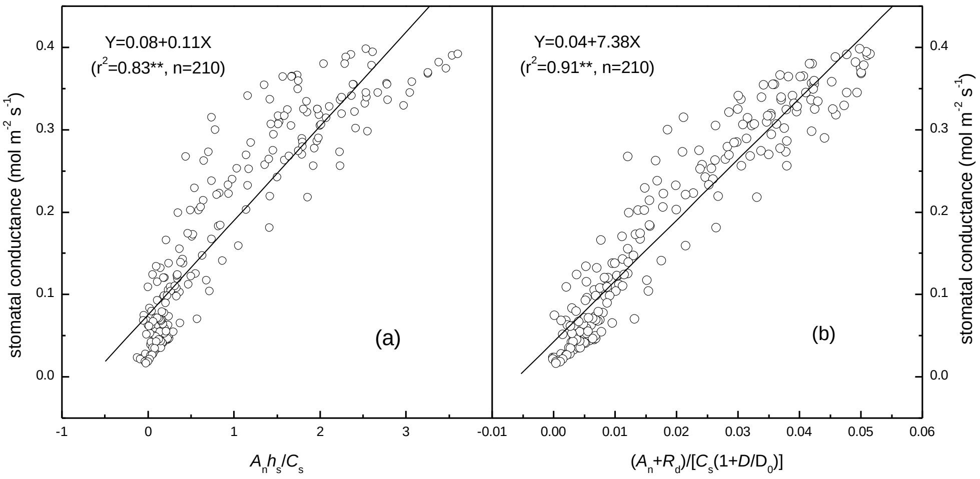

Y=0.08+0.11X
(r^2=0.83**, n=210)
(a)
Y=0.04+7.38X
(r^2=0.91**, n=210)
(b)
stomatal conductance (mol m^{-2} s^{-1})
0.0
0.1
0.2
0.3
0.4
-1
0
1
2
3
$A_n h_s/C_s$
-0.01
0.00
0.01
0.02
0.03
0.04
0.05
0.06
$(A_n+R_d)/[C_s(1+D/D_0)]$

Fig. 3

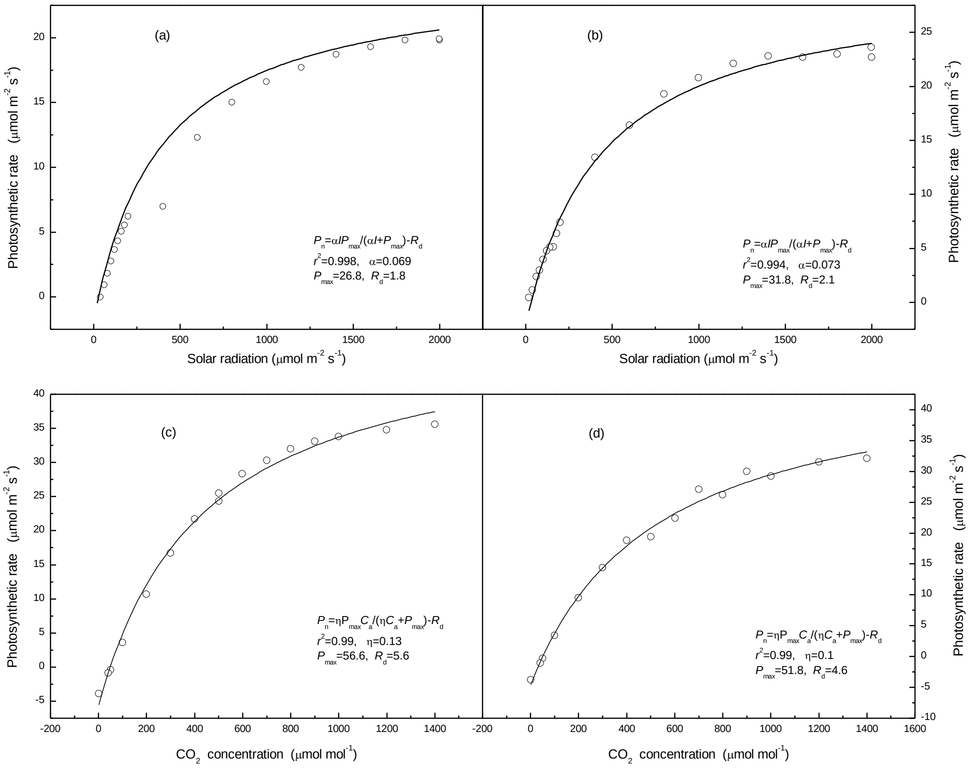

(a)
(b)
(c)
(d)
Photosynthetic rate (μmol m-2 s-1)
Solar radiation (μmol m-2 s-1)
CO2 concentration (μmol mol-1)
Pn=αIPmax/(αI+Pmax)-Rd
r2=0.998, α=0.069
Pmax=26.8, Rd=1.8
Pn=αIPmax/(αI+Pmax)-Rd
r2=0.994, α=0.073
Pmax=31.8, Rd=2.1
Pn=ηPmaxCa/(ηCa+Pmax)-Rd
r2=0.99, η=0.13
Pmax=56.6, Rd=5.6
Pn=ηPmaxCa/(ηCa+Pmax)-Rd
r2=0.99, η=0.1
Pmax=51.8, Rd=4.6
0
5
10
15
20
25
30
35
40
-5
-10
500
1000
1500
2000
-200
200
400
600
800
1000
1200
1400
1600

Fig. 4

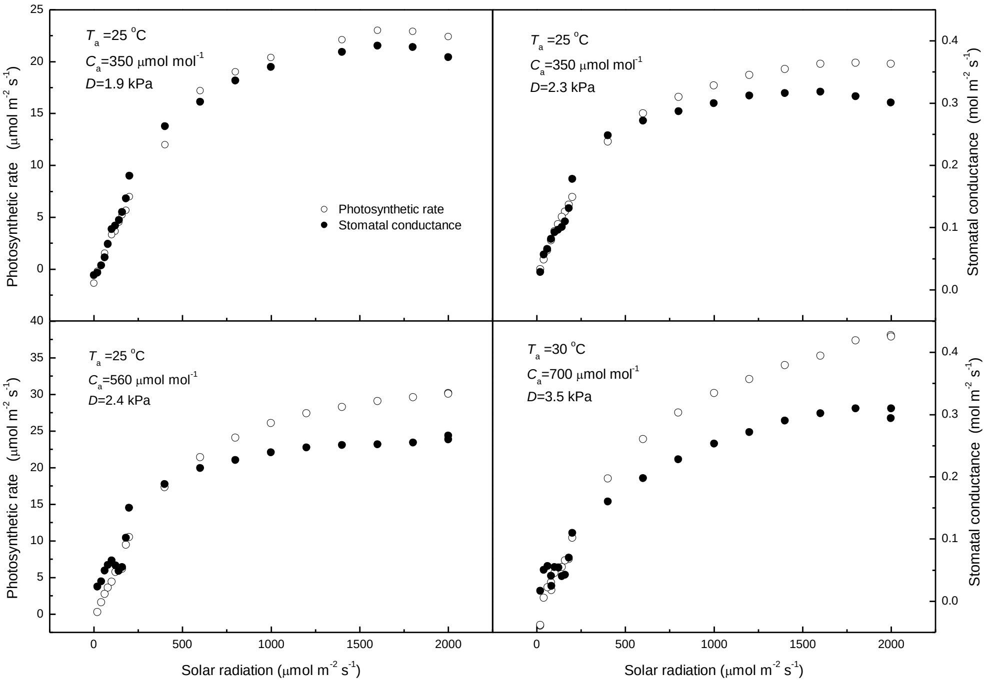

T_a =25 °C
C_a=350 μmol mol^{-1}
D=1.9 kPa
T_a =25 °C
C_a=350 μmol mol^{-1}
D=2.3 kPa
T_a =25 °C
C_a=560 μmol mol^{-1}
D=2.4 kPa
T_a =30 °C
C_a=700 μmol mol^{-1}
D=3.5 kPa
○ Photosynthetic rate
● Stomatal conductance
Photosynthetic rate (μmol m^{-2} s^{-1})
Stomatal conductance (mol m^{-2} s^{-1})
Solar radiation (μmol m^{-2} s^{-1})
0
5
10
15
20
25
30
35
40
0.0
0.1
0.2
0.3
0.4
0
500
1000
1500
2000

Fig. 5

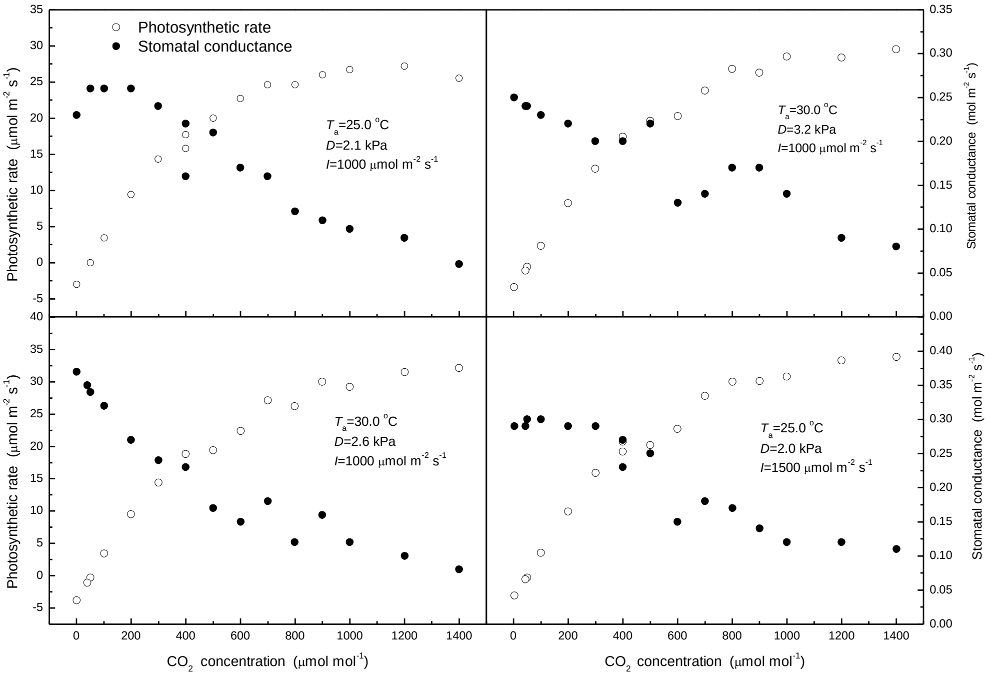

Photosynthetic rate
Stomatal conductance
T_a=25.0 °C
D=2.1 kPa
I=1000 μmol m^{-2} s^{-1}
T_a=30.0 °C
D=3.2 kPa
I=1000 μmol m^{-2} s^{-1}
T_a=30.0 °C
D=2.6 kPa
I=1000 μmol m^{-2} s^{-1}
T_a=25.0 °C
D=2.0 kPa
I=1500 μmol m^{-2} s^{-1}
Photosynthetic rate (μmol m^{-2} s^{-1})
Stomatal conductance (mol m^{-2} s^{-1})
CO$_2$ concentration (μmol mol^{-1})
-5
0
5
10
15
20
25
30
35
40
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0
200
400
600
800
1000
1200
1400

Fig. 6

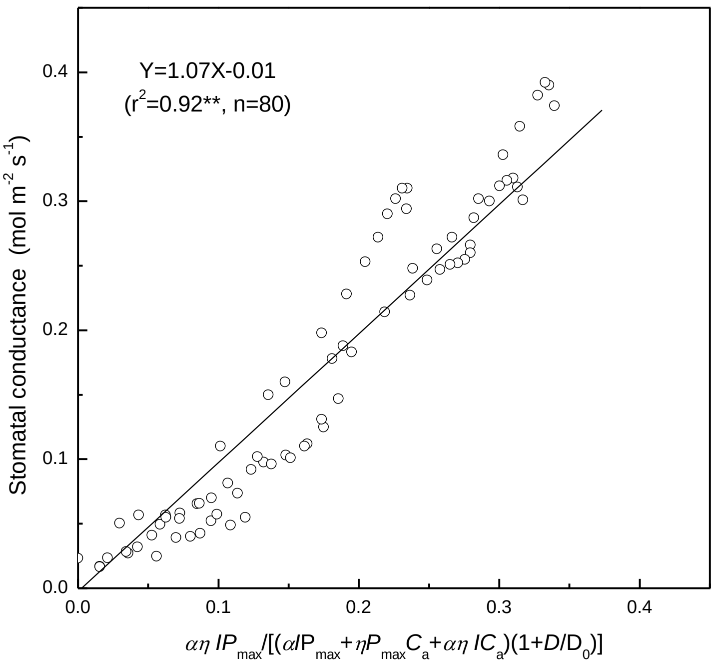
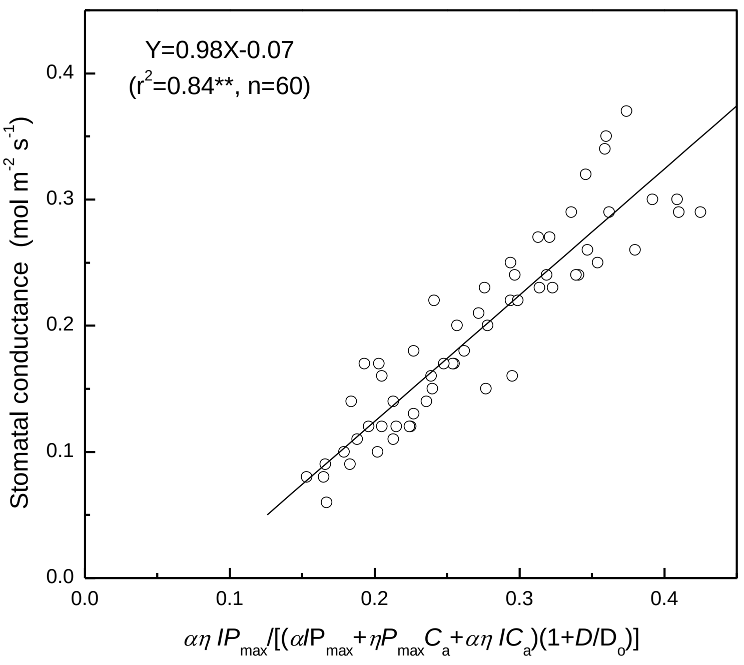

Y=1.07X-0.01
(r^2=0.92**, n=80)
Stomatal conductance (mol m^{-2} s^{-1})
0.0
0.1
0.2
0.3
0.4
0.0
0.1
0.2
0.3
0.4
$\alpha\eta\ IP_{max}/[(\alpha I\mathrm{P}_{max}+\eta P_{max}C_a+\alpha\eta\ IC_a)(1+D/\mathrm{D}_0)]$

Fig. 7


Y=0.98X-0.07
(r^2=0.84**, n=60)
Stomatal conductance (mol m^{-2} s^{-1})
0.0
0.1
0.2
0.3
0.4
0.0
0.1
0.2
0.3
0.4
$\alpha\eta\, IP_{max}/[(\alpha I P_{max}+\eta P_{max}C_a+\alpha\eta\, IC_a)(1+D/D_o)]$