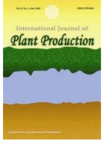

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A modified optimal stomatal conductance model under water-stressed condition

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Abstract

Accurate estimation of leaf stomatal conductance (g_s) is important in predicting carbon and water cycles of terrestrial ecosystem. To estimate g_s on field-grown soybean and maize under water-stressed condition accurately, a modified optimal stomatal conductance (OSCM) model was established based on the relationship between marginal water cost of carbon gain and soil water content by introducing a water stress factor ($f(\theta_v)$). $f(\theta_v)$ had same form with that in Jarvis and Ball-Berry-Leuning (BBL) models. The OSCM model was evaluated and compared with the original optimal stomatal conductance (OSC), Jarvis and BBL models by comparing observed and estimated g_s of three-year data on soybean and four-year data on maize in an arid region of northwest China. Results show that the OSCM and OSC models were more steady and accurate than the Jarvis and BBL models for estimating g_s on soybean and maize at the different years. Moreover, the OSCM model performed better than the OSC model because of considering the effect of water stress. Compared with the OSC, Jarvis and BBL models, the OSCM model improved the accuracy of estimating g_s on soybean and maize on average by 7%, 25% and 35% and reduced the RMSE by 19%, 56% and 43%, respectively. As for estimating diurnal change of g_s on soybean and maize under both well-watered and water-stressed conditions, the OSCM model also performed better than the OSC, Jarvis and BBL models. Under water-stressed condition, only the OSCM model is recommended due to its high accuracy, conservative and accessible parameter, which can provide a more accurate and convenient tool in predicting water and carbon fluxes of terrestrial ecosystem in the arid area.

Keywords: Optimal stomatal regulation; Marginal water cost of carbon gain; Soil water content; Jarvis; BBL.

Introduction

Leaf stomata is the main channel of water and carbon exchange between plants and environment and it can regulate water loss by transpiration and CO_2 uptake by photosynthesis (Hetherington and Woodward, 2003). So accurate estimation of leaf stomatal conductance (g_S) is very important in analyzing CO_2 and H_2O fluxes of ecosystem and the global carbon and water cycles under the changing environmental condition (Van Wijk et al., 2002; Berry et al., 2010).

Now the widely used stomatal conductance model has been divided into two types. One is empirical 'multiplicative' model of environmental influences (Jarvis, 1976). And it supposes that the response of each environmental factor such as photosynthetically active radiation (*PAR*), temperature (*T*), relative humidity (*RH*), ambient CO_2 concentration (C_a) and water status (soil water content θ_v or soil/leaf water potential ψ) to g_s is independent and also the impacts of environmental factors on g_s are synergic. Many researches have improved and optimized the forms and functions of stomatal response to environmental variables in the subsequent application of the Jarvis model (Stewart, 1988; Dolman, 1993; Ogink-Hendriks, 1995; White et al., 1999; Macfarlane et al., 2004; Noe and Giersch, 2004). The other is semi-empirical and semi-mechanistic model. Based on the linear relationship between g_s and photosynthesis from stomatal behavior experiment (Wong et al., 1978) and combined with the response of stomata to C_a and RH, thus the semi-empirical and semi-mechanistic model of Ball-Berry (BB) was established (Ball et al., 1987). And then Ball-Berry-Leuning (BBL) model was obtained by introducing CO_2 compensation point and replacing relative humidity with saturated vapor pressure deficit based on leaf temperature (Leuning, 1990; 1995) and was widely used. Many studies have modified the BB and BBL model by considering the impact of water stress on g_s (Sala and Tenhunen, 1996; Wang and Leuning, 1998; Van Wijk et al., 2000; Tuzet et al., 2003; Misson et al., 2004; Uddling et al., 2005; Liu et al., 2009; Mueller et al., 2014). Whether empirical model (Jarvis, 1976; Stewart, 1988; Macfarlane et al., 2004; Misson et al., 2004) or semi-empirical model (Wang and Leuning, 1998; Van Wijk et al., 2000; Tuzet et al., 2003; Misson et al., 2004), the influence of water stress on g_s is often characterized by water status (soil water content θ, or soil water potential ψ_s, or leaf water potential ψ_l). In order to obtain the parameters of the model more accessible, this study chose soil water content to represent water status of the plant.

A new optimal stomatal conductance (OSC) model was proposed a few years ago (Medlyn et al., 2011) and considered as mechanistic model (Keenan et al., 2013). The OSC model is obtained on the basis of optimization theory of stomatal regulation (Cowan and Farquhar, 1977) through coupling with biophysical and biochemical processes of photosynthesis and transpiration (Arneth et al., 2002). Compared with the semi-empirical BBL model, the OSC model has only one parameter (g_l^*) that relies on the calculation of marginal water cost of carbon gain (λ), which is the key parameter in optimization theory of stomatal regulation. However, the quantitative relationships of λ and soil moisture is still lacking (Katul et al., 2010) and λ is difficult to obtain directly from the environmental variables, which limits the application of the model. Although the OSC model is a mechanistic model of stomatal conductance, the parameters (g_l^*) in the model is still obtained by empirical fitting method in the current application (Heroult et al., 2013; Zhou et al., 2013; De Kauwe et al., 2015; Lin et al., 2015). And the OSC model is mainly applied in natural vegetation, rarely in crops (Medlyn et al., 2011; De Kauwe et al., 2013; Zhou et al., 2013; De Kauwe et al., 2015; Lin et al., 2015).

The objectives of this study were to (1) propose a modified optimal stomatal conductance model (OSCM) considering the quantitative relationship of marginal water cost of carbon gain (λ) and soil water content (θ_v), (2) compare the performance of the OSCM model with that of Jarvis, BBL and original optimal stomatal conductance (OSC) models in the arid region and choose the fittest stomatal conductance model.

Model descriptions

Jarvis model

The form of Jarvis model is as follows:

$$g_s = g_m f_1(PAR) f_2(T) f_3(VPD) f_4(C_a) f_5(\theta_v) \tag{1}$$

where g_s is the stomatal conductance to H_2O, g_m is the maximum stomatal conductance, T is the leaf temperature, VPD is the leaf-to-air vapor pressure deficit, θ_v is the volumetric soil water content in the root zone. This study did not consider the impact of CO_2 on stomatal conductance because the concentration of CO_2 fluctuates slightly under natural experimental condition, so $f_4(C_a)$ takes 1. As for $f_1(PAR)$, $f_2(T)$, $f_3(VPD)$ and $f_5(\theta_v)$, the response functions of stomatal conductance to PAR, T, VPD and θ_v are as follows (Jarvis, 1976; Stewart, 1988; Massman and Kaufmann, 1991; Dolman, 1993):

$$f_1(PAR) = \frac{PAR}{PAR + Q_0} \tag{2}$$

$$f_2(T) = 1 - t_1 (T - T_o)^2 \tag{3}$$

$$f_3(VPD) = \frac{1}{1 + \left(VPD / \mathrm{d}_1 \right)^{d_2}} \tag{4}$$

$$f_5(\theta_\mathrm{v}) = \begin{cases} 0 & \theta_v < \theta_w \\ \dfrac{\theta_v - \theta_w}{\theta_f - \theta_w} & \theta_w \le \theta_v \le \theta_f \\ 1 & \theta_v > \theta_f \end{cases} \tag{5}$$

where Q_0 is photosynthetically active radiation at half of the maximum stomatal conductance and Q_0 takes 402 and 390 mol m^{-2} s^{-1} for soybean and maize, respectively, according to the measured A-PAR response curve. T_o is the optimal leaf temperature and t_1 is the curvature of response curve of temperature to stomatal conductance. θ_w and θ_f are the volumetric soil water contents (m^3 m^{-3}) at wilting point and field capacity in the root zone. According to our measured and previous data, the main root zone is distributed in the depth of 0-60 cm for soybean (our unpublished data) and 0-100 cm for maize (Wu et al., 2016). t_1, d_1 and d_2 are fitted parameters.

Ball-Berry-Leuning (BBL) model

The BBL model was developed based on the linear relationship of stomatal conductance and net photosynthesis rate under well-watered condition (Leuning, 1995) and its form is as follows:

$$g_s = g_0 + g_1 \frac{A}{(C_a - \Gamma)\left(1 + {VPD}/{VPD_0}\right)} \tag{6}$$

where g_0 is the stomatal conductance to H_2O at zero photosynthesis, a constant near 0 (Leuning, 1995; Tuzet et al., 2003) and g_0 takes 0 in this study. g_l is a fitted parameter, VPD_0 is a characteristic parameter reflecting the response of stomata to vapor pressure deficit, A is the net photosynthesis rate, C_a is ambient CO_2 concentration. Γ is the CO_2 compensation point of photosynthesis and it takes 55 and 6.5 µmol mol^{-1} for soybean and maize, respectively according to the measured A-Ci response curve.

Considering the impact of water stress on stomatal conductance, soil water stress factor $f_5(\theta_v)$, which has similar meaning to that in Jarvis model, is introduced, then the modified BBL model is obtained by multiplying $f_5(\theta_v)$ on the basis of formula (6), as follows:

$$g_s = g_1 f_5(\theta_v) \frac{A}{(C_a - \Gamma)\left(1 + {VPD}/{VPD_0}\right)} \tag{7}$$

Optimal stomatal conductance model (OSC)

The optimal stomatal conductance model (OSC) is developed from an understanding of the mechanism based on stomatal regulation optimization theory (Medlyn et al., 2011). The theory is from the evolution opinion of stomata (Cowan and Farquhar, 1977; Cowan, 2002). And it assumes that stomata should behave to maximize total carbon assimilation or minimize total transpiration in response to environmental factors over a period of time to obtain the highest water use efficiency. The OSC model has combined the theory with biophysical and biochemical processes of transpiration and photosynthesis and is different from phenomenological empirical approaches. And the OSC model assumes that stomata behave as they optimize for RuBP (ribulose-1, 5 biphosphate) regeneration-limited photosynthesis rather than Rubisco-limited photosynthesis (Medlyn et al., 2011), the form of the OSC model is as follows:

$$g_s = g_0 + 1.6\left(1 + \frac{g_1^*}{\sqrt{VPD/P}}\right)\frac{A}{C_a} \tag{8}$$

$$g_1^* = \sqrt{3\Gamma\lambda/1.6} \tag{9}$$

where g_0 has similar meaning with that of BBL model and can be ignored (Lin et al., 2012; De Kauwe et al., 2013; Heroult et al., 2013), P is average atmospheric pressure taking 84 KPa and the remaining symbols has the same meaning as before.

The only parameter (g_l^*) in the OSC model depends on the marginal water cost of carbon gain (λ) and λ is defined from physiological significance as follows:

$$\lambda = \frac{\partial E / \partial g_s}{\partial A / \partial g_s} \tag{10}$$

where E and A are leaf transpiration rate and net photosynthesis rate, $\partial E/\partial g_s$ and $\partial A/\partial g_s$ are the sensitivity of stomatal conductance to transpiration rate and photosynthetic rate, respectively.

The Eq. (10) shows that λ is difficult to obtain directly from the environmental factors, so it is obtained by fitting the model. λ in the OSC model takes λ_{max}, which represents the marginal water cost of carbon gain under well-watered condition and not considering the impacts of soil water content during the growing season. λ_{max} was obtained by fitting the OSC model using the gas exchange data under well-watered condition in 2012 (51 groups for soybean, 31 groups for maize). And it takes 5250 and 4204 mol H_2O mol^{-1} CO_2 for soybean and maize, respectively.

Modified optimal stomatal conductance model (OSCM) considering the relationship of marginal water cost of carbon gain and soil water content

Some studies demonstrate that λ is mainly related to plant functional type and soil water content (the changes of CO_2 concentration is not considered in this study during a relatively short time under natural condition) and λ is proportional to soil water content (Hall and Schulze, 1980; Thomas et al., 1999; Arneth et al., 2002; Katul et al., 2012). Therefore, the quantitative relationship between λ and soil water content θ_v is assumed as follows:

$$\lambda = \lambda_{\max} f\left(\theta_v\right) \tag{11}$$

where λ_{max} is the same as that in the OSC model. The water stress factor ($f(\theta_v)$) is the same as that in the Jarvis and BBL models ($f_5(\theta_v)$). And $f_5(\theta_v)$ tended to 1 around the field capacity while it was close to 0 at near wilting point for soybean and maize.

Putting the formula (11) into (9) and (8) of the OSC model, the modified optimal stomatal conductance model (OSCM) considering the relationship between marginal water cost of carbon gain (λ) and root-zone soil water content (θ_v) is obtained and its form is as follows:

$$g_s = \left(1.6 + \frac{\sqrt{4.8\Gamma\lambda_{\max} f\left(\theta_v\right)}}{\sqrt{VPD/P}}\right)\frac{A}{C_a} \tag{12}$$

where Γ, A, C_a, VPD and P have the same meanings as those of the former models.

Materials and Methods

Study site

The field experiments were carried out during 2012-2015 seasons at Shiyanghe Experimental Station for Water-saving in Agriculture and Ecology of China Agricultural University (37° 52' N, 102° 50' E, 1581 m a.s.l.), located in Wuwei city, Gansu Province of northwest China. It is in a temperate continental climate region, where light and heat resources are rich, the difference of temperature between day and night is huge, average annual sunshine duration is over 3000 h, the frost-free days is 150 d and annual accumulated temperature (over 0 ºC) is over 3550 degree-day, while annual precipitation is 164.5 mm and annual pan evaporation is 2000 mm during the year 1951-2013 (Jiang et al., 2016).

The soybean (*Glycine max* L. Merr.) experiment was conducted in 2012, 2013 and 2015 and the cultivar is zhonghuang 30, which widely planted in local area. Soybean was sown on May 10, May 10 and May 7 and harvested on September 20, September 17 and September 15 in 2012, 2013 and 2015, respectively. The soybean was planted in east-west rows with a distance between and within rows of 50 cm and 15 cm, with drip irrigation under plastic mulch. Two rows plants were planted in one plastic film symmetrically and irrigated by one drip tape located in the center of plastic film, with sowing in dry soil and germination in wet soil. The soil texture is a sandy loam in the depth of 0.6 m, with a mean soil dry bulk density of 1.48 g/cm^3 and soil water content at field capacity and wilting point of 0.26 and 0.08 m^3 m^{-3}, respectively.

The maize (*Zea mays* L. cultivar Funong 963) experiment was carried out in 2012, 2013, 2014 and 2015, sown on April 16, April 13, April 16 and April 15 and harvested on September 20, September 12, September 20 and September 16, respectively. Maize was planted in east-west rows with a distance between and within rows of 40 cm and 22 cm, with border irrigation under plastic mulch. The soil texture is a clay loam in the depth of 1.0 m, with a mean soil dry bulk density of 1.38 g/cm^3 and soil water content at field capacity and wilting point of 0.30 and 0.12 m^3 m^{-3}, respectively.

Measurements

Gas exchange

After the random selection of fully developed upper leaves from healthy plants in sunny or cloudy days, photosynthetic parameters including g_s, A, E, T and RH, A-Ci response curve and A-PAR response curve were measured using an open portable photosynthesis system LI-6400 (Li-Cor, Lincoln, NE, USA).

Diurnal change of gas exchange parameters was measured every 1 h from 8: 00 to 20: 00 in sunny day using standard leaf chamber (6 cm^2) under natural condition once or twice during each growth stage of soybeans and maize (except seedling stage, because the leaves were too small and plants were too short leading to measure inconveniently) depending on weather condition. In addition, gas exchange parameters for two days with significant difference of soil water content were measured from 09: 00 to 11: 00 at each growth stage (except seedling stage) when transpiration and photosynthesis are strong.

The A-PAR response curve and the A-Ci response curve of soybean and maize were measured during July and August in 2015, using red-blue LED light source (6400-02B) with CO_2 injector system (6400-01) to eliminate the influence of ambient air fluctuation. The A-PAR response curve was conducted at PAR of 2000, 1800, 1500, 1200, 1000, 800, 600, 400, 200, 100, 50, 20 and 0 μmol m^{-2} s^{-1} under CO_2 concentration of 400 μmol m^{-2} s^{-1} and the measured leaves were adapted for 0.5 h at saturated PAR of 1800 μmol m^{-2} s^{-1}. The A-Ci response curve was measured at CO_2 concentrations of 400, 300, 200, 150, 100, 50, 400, 400, 600, 800, 1000, 1200, 1500, 1800 and 2000 μmol mol^{-1} at saturated PAR and leaf temperature of 30 ºC after measured leaves were adapted for 0.5 h at saturated PAR and 400 μmol m^{-2} s^{-1} CO_2. Saturated PAR was kept at 1800 μmol m^{-2} s^{-1} for soybean and maize according to the measured A-PAR response curves. The fitness of A-Ci response curves are referred to Farquhar-equation (Long and Bernacchi, 2003; Sharkey et al., 2007) and A-PAR response curves are referred to modified hyperbolic curve (Ye et al., 2013).

Soil water content

Volumetric soil water contents for soybean in 2012 and 2013 and for maize in 2012, 2013 and 2014 were measured by Diviner 2000 system (Sentek Pty Ltd., Australia) and were calibrated using gravimetric method. One PVC access tube was installed in the depths of 0.6 and 1.0 m for soybean and maize, respectively. Measurements were made at the interval of 0.1 m every 5-7 days. Soil water contents for soybean and maize in 2015 were continuously monitored using five EC-5 sensors (Decagon Devices Inc., Pullman, WA, USA) and collected every 30 min using EM50 data-logger (Decagon Devices Inc., Pullman, WA, USA) at the interval of 0.2 m in the depths of 0.6 and 1.0 m and were also calibrated using gravimetric method.

Meteorological data

Precipitation, solar radiation (R_a), air temperature (T_a), wind speed at 2 m above ground and wind direction and relative humidity (RH), were continuously monitored using a standard automatic weather station (Hobo, Onset Computer Corp., USA) about 100 and 30 m away from the experimental soybean and maize field. All data were taken at the interval of 5 s and recorded at a 15-min interval. Table 1 summarizes the main meteorological parameters during the soybean and maize growing seasons of each year.

Table 1. Summary of yearly meteorological variables during the growing seasons of soybean and maize in 2012-2015. Precipitation is the sum of the whole growing season, and the other meteorological variables are the daily average value during the whole growing season.

Crop Type	Year	Precipitation	T_a	T_{max}	T_{min}	Wind speed	VPD	R_a	RH
		mm	ºC	ºC	ºC	m s^{-1}	kPa	W m^{-2}	%
Soybean	2012	118	18.0	23.0	13.0	0.69	1.27	270	49.1
	2013	62	20.1	27.3	12.8	0.48	1.46	207	55.6
	2015	146	19.5	27.3	12.1	0.62	1.45	229	55.2
Maize	2012	129	17.0	21.8	12.3	0.85	1.22	264	47.5
	2013	68	19.4	26.7	12.1	0.55	1.47	211	51.8
	2014	220	17.9	25.3	10.6	0.62	1.28	222	57.4
	2015	154	18.7	26.5	11.3	0.71	1.43	226	52.4

Table 2. List of variables for four models.

Symbols	Unit	Definition
g_s	mol H_2O m^{-2} s^{-1}	Stomatal conductance to water vapor
PAR	μmol m^{-2} s^{-1}	Photosynthetically active radiation
T	ºC	Leaf temperature
VPD	kPa	Leaf-to-air vapor pressure deficit
C_a	μmol mol^{-1}	Ambient CO_2 concentration
θ_v	m^3 m^{-3}	Root-zone volumetric soil water content
A	μmol CO_2 m^{-2} s^{-1}	Leaf photosynthesis rate
E	mmol H_2O m^{-2} s^{-1}	Leaf transpiration rate
λ	mol $H_2O \cdot mol^{-1}$ CO_2	Marginal water cost of carbon gain

Data analysis and evaluation of model performance

1^{st} Opt (First Optimization, 7D-Soft High Technology Inc., China) was used to fit parameters of models by Levenberg-Marquardt and Universal Global Optimization – UGO methods. The A-PAR and A-Ci response curves were fitted by Photosynthesis (Li-Cor Inc., Lincoln, NE, USA).

The performance of the model is mainly evaluated by the linear regression equation between the estimated and measured values. In this study, model slope (b_0), determination coefficient (R^2), mean absolute bias error (MAE) and root mean square error (RMSE) were used and they were calculated as follows (Willmott, 1982; Chai and Draxler, 2014; Pereira et al., 2015):

$$b_0 = \frac{\sum_{i=1}^{n} O_i E_i}{\sum_{i=1}^{n} O_i^2} \tag{13}$$

$$R^2 = \left[\frac{\sum_{i=1}^{n}\left(O_i - \bar{O}\right)\left(E_i - \bar{E}\right)}{\sqrt{\sum_{i=1}^{n}\left(O_i - \bar{O}\right)^2}\sqrt{\sum_{i=1}^{n}\left(E_i - \bar{E}\right)^2}} \right]^2 \tag{14}$$

$$MAE = \frac{1}{n}\sum_{i=1}^{n}\left|O_i - E_i\right| \tag{15}$$

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(O_i - E_i\right)^2} \tag{16}$$

where O_i and E_i are the observed and estimated values, respectively, $\bar{O}$ and $\bar{E}$ are the average observed and estimated values, respectively, n is sampling number.

Results and Discussion

Calibration of four models

The Jarvis and BBL models were parameterized by fitting the Eqs. (1) - (7) to gas exchange data of soybean and maize in 2012 and the results are shown in Table 3. Based on the estimated values of parameters, replacing the observed gas exchange data of 2012 for soybean and maize into the Eqs. (2) - (5) found that the values of *f*(*PAR*), *f*(*T*) and *f*(*VPD*) were all between 0-1, which demonstrates that the estimated values of parameters in the Jarvis model were reasonable. The values of g_l and VPD_0 in the BBL model were within the expected range in terms of their biological meaning.

Table 3. List of constants for four models.

Symbols	Value (Soybean)	Value (Maize)	Unit	Source	Model	Definition
θ_w	0.08	0.12	$m^3\ m^{-3}$	Measured	All	Root-zone volumetric soil water content at wilting point
θ_f	0.26	0.30	$m^3\ m^{-3}$	Measured	All	Root-zone volumetric soil water content at field capacity
g_m	1.25	1.1	$mol\ m^{-2}\ s^{-1}$	Fitted	Jarvis	Maximum stomatal conductance
Q_0	402	390	$\mu mol\ m^{-2}\ s^{-1}$	Measured	Jarvis	Photosynthetically active radiation at half of maximum stomatal conductance
T_0	32	33	ºC	Fitted	Jarvis	Optimal leaf temperature
t_1	0.002	0.0001	-	Fitted	Jarvis	Fitted parameter
d_1	2.5	3.81	kPa	Fitted	Jarvis	Fitted parameter
d_2	2.7	3.54	-	Fitted	Jarvis	Fitted parameter
g_l	16.01	16.28	-	Fitted	BBL	Fitted parameter
VPD_0	2.49	2.83	kPa	Fitted	BBL	Fitted parameter
P	84	84	kPa	Measured	BBL, OSC, OSCM	Average local atmospheric pressure
g_0	0	0	$mol\ m^{-2}\ s^{-1}$	De Kauwe et al. (2015)	BBL, OSC, OSCM	Minimum stomatal conductance
Γ	55	6.5	$\mu mol\ CO_2\ mol^{-1}$	Measured	BBL, OSC, OSCM	CO_2 compensation point in the absence of dark respiration
λ_{max}	5250	4204	$mol\ H_2O \cdot mol^{-1}\ CO_2$	Fitted	OSC, OSCM	Maximum marginal water cost of carbon gain

For the two optimal models (OSC and OSCM), one point should be noted that the response expression of stomata to VPD is VPD/P (Misson et al., 2004), but P is often omitted and implied in g_l^* in the previous studies (Medlyn et al., 2011; Lin et al., 2012; Zhou et al., 2013; Lin et al., 2015). In this study, in order to clearly understand the response of g_s to environmental variables, P and g_l^* was separated, so g_l^* in the studies of Zhou et al. (2013) and Lin et al. (2015) is $\sqrt{P}$ times than that in this study (P is 84 kPa in this study). λ_{max} in the two optimal g_s models for soybean and maize was 5250 and 4204 mol H_2O mol^{-1} CO_2 and corresponding g_l^* was 0.58 and 0.18, which is close to the results of Lin et al. (2015) (average estimated value of g_l^* for C_3 and C_4 is 5.79 and 1.62 kPa$^{0.5}$ in Lin et al. (2015), but g_l^* for C_3 and C_4 divided by $\sqrt{84}$ kPa$^{0.5}$ is 0.63 and 0.18 in this study, respectively).

The parameters in four models, Γ and λ_{max} were significantly different for soybean and maize. Γ, the CO_2 compensation point of photosynthesis, for maize was 6.5 μmol mol^{-1}, significantly lower than 55 μmol mol^{-1} for soybean. The difference is mainly because maize which is a C_4 plant has efficient utilization of low CO_2 concentration than soybean, a C_3 plant. λ_{max}, maximum marginal water cost of carbon gain, is inversely proportional to water use efficiency. Therefore, that λ_{max} for maize is lower than that for soybean is probably because C_4 plant has higher water use efficiency than C_3 plant.The four models showed good agreement with observations over the calibration period (2012 data) both for soybean and maize (Tables 4 and 5, Figure 1 (a,b,c,d) and Figure 2 (a,b,c,d)). The slopes of the linear regression between observed and estimated data ranged from 0.81 (Jarvis model) to 0.99 (OSC and OSCM model) and the R^2 ranged from 0.51(Jarvis model) to 0.92 (OSC and OSCM model). So it was obvious that the two optimal models (OSC and OSCM) had the best goodness-of-fit for soybean and maize during the calibration period, BBL model followed and Jarvis model had the worst. The estimating accuracy of the OSC and OSCM models for soybean and maize were 0.99 and 0.92, respectively, which had 4% and 2% higher than BBL model and 5% and 14% higher than Jarvis model, respectively.

Table 4. Performance of four models on soybean. b_0 and R^2 are the coefficients of regression and determination, respectively; RMSE is the root mean square error; MAE are the mean absolute bias error.

Year	Model	b_0	R^2	RMSE (mmol m^{-2}s^{-1})	MAE (mmol m^{-2}s^{-1})	n
2012 (Calibration)	Jarvis	0.94	0.79	110	83	278
	BBL	0.95	0.87	86	59	278
	OSC/ OSCM	0.99	0.92	70	57	51
2013 (Validation)	Jarvis	0.65	0.56	149	128	367
	BBL	0.72	0.66	124	105	367
	OSC	1.12	0.65	98	77	367
	OSCM	0.90	0.70	76	60	367
2015 (Validation)	Jarvis	0.88	0.41	99	69	380
	BBL	0.84	0.76	58	37	380
	OSC	1.15	0.86	57	42	380
	OSCM	0.98	0.84	46	30	380

Table 5. Performance of four models on maize. The symbols b_0, R^2, RMSE, MAE are the same with Table 4.

Year	Model	b_0	R^2	RMSE ($mmol\ m^{-2}s^{-1}$)	MAE ($mmol\ m^{-2}s^{-1}$)	n
2012 (Calibration)	Jarvis	0.81	0.51	74	55	324
	BBL	0.90	0.80	55	45	324
	OSC/ OSCM	0.92	0.88	53	39	31
2013 (Validation)	Jarvis	1.43	0.47	135	114	638
	BBL	1.83	0.80	191	164	638
	OSC	1.24	0.85	67	60	638
	OSCM	1.13	0.86	46	39	638
2014 (Validation)	Jarvis	1.26	0.50	142	102	312
	BBL	1.42	0.82	122	86	312
	OSC	1.08	0.86	55	44	312
	OSCM	0.94	0.86	48	34	312
2015 (Validation)	Jarvis	1.80	0.64	277	247	76
	BBL	2.21	0.90	362	315	76
	OSC	1.03	0.88	49	40	76
	OSCM	1.01	0.88	48	39	76

Validation and comparison of four models

Comparison of estimated and observed stomatal conductance for soybean and maize during the whole growing season in different years

The four models were validated with the data of 2013 and 2015 for soybean and 2013, 2014 and 2015 for maize. The linear relationships between the estimated and measured g_s are shown in Figures 1 and 2 and the goodness-of-fit indicators of the models are shown in Tables 4 and 5. From Figure 1 (e - l), estimated g_s of soybean in 2013 and 2015 by OSCM model were close to the measured value, but the OSC model overestimated g_s slightly and the Jarvis and BBL models underestimated it significantly. From Table 4, the OSCM model gave the best accuracy with lowest error in estimating g_s of soybean, the OSC model followed and the BBL model had better estimation accuracy than the Jarvis model. In the case of estimating g_s of soybean in 2015, the OSC model overestimated it by 15% and the Jarvis and BBL models underestimated it by 12% and 16%, but the OSCM model underestimated it just by 2%. And also the RMSE for the OSCM model, 76 and 46 mmol m^{-2} s^{-1} respectively for 2013 and 2015 seasons, were lower than the OSC, Jarvis and BBL models by 22% and 19%, 49% and 53% and 39% and 19%, respectively.As can be seen from Figure 2 (e - p), for estimating g_s of maize in 2013, 2014 and 2015, the two optimal models (OSC and OSCM) estimated them accurately while the Jarvis model overestimated them with a discrete scatter diagram and the BBL model overestimated it with a gathering scatter diagram. From Table 5, for estimating g_s of maize in 2013, 2014 and 2015, the OSCM model gave the best accuracy, but the Jarvis and BBL models overestimated them by 50% and 82% on average. The OSC model performed very well as the OSCM model did in 2015, but overestimated g_s by 24% in 2013. This is because the soil water content was very ample in 2015 (θ_v is 0.28-0.29 m^3 m^{-3}) and water stress factor was close to 1, so the difference of estimated g_s by the OSC and OSCM models was slight whether considering water stress or not. In 2013, the soil water content θ_v ranged from 0.17 to 0.30 m^3 m^{-3} and g_s under water-stressed condition was included, so the water stress factor $f_5(\theta_v)$ was less than 1, thus the OSC model overestimated g_s because of ignoring the water stress effect. From Table 4 and Figure 1 (b, f, j), the BBL model significantly underestimated g_s with high R^2 in calibration period although it performed well in calibration period for soybean. From Table 5 and Figure 2 (b, f, j, n), there was a similar case for maize and the BBL model overestimated g_s for maize with high R^2 in calibration period. The high R^2 shows that the BBL model captures the main response of stomata to environmental factors. However, the BBL model was not stable in estimating g_s among different seasons because its parameter g_l correlated with meteorological conditions. Compared with g_l in the BBL model, the optimal models (OSC and OSCM) performed well in both calibration and validation seasons. This is because the only parameter λ_{max} for soybean and maize was more stable among different seasons. The parameter in stomatal conductance model being stable is very important when predicting stomatal conductance and transpiration at canopy or larger scales. Replacing the optimal stomatal conductance model with the BBL model in the land surface model of Community Atmosphere Biosphere Land Exchange can reduce annual fluxes of transpiration by 30% (De Kauwe et al., 2015).

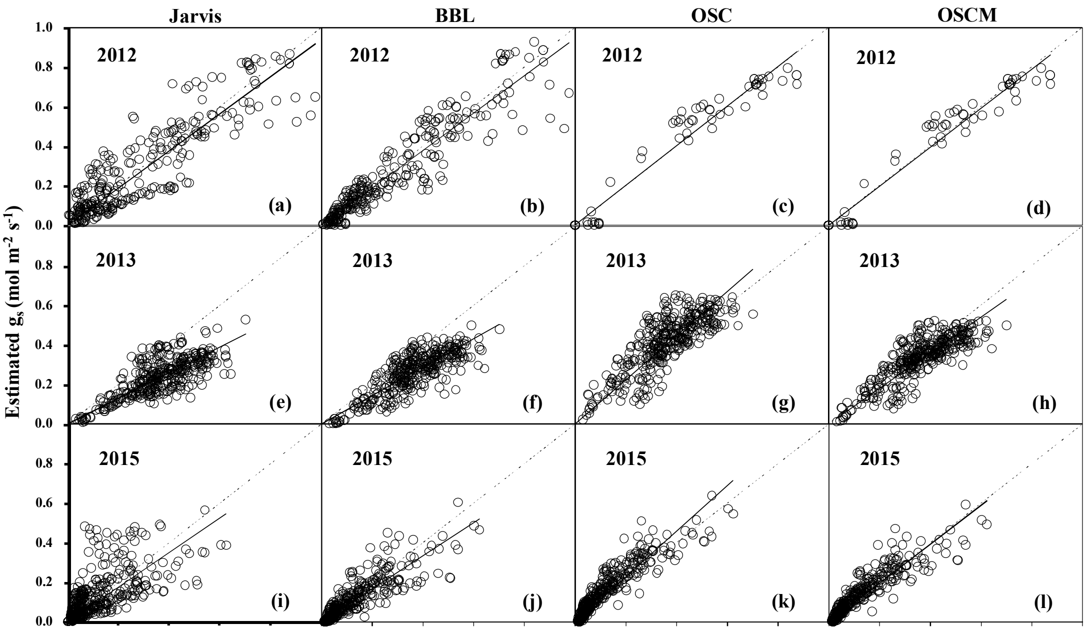

Figure 1. Comparison of observed and estimated stomatal conductance (g_s) by four models on soybean in 2012, 2013 and 2015. Calibration: a-d, validation: e-l, in which c and d are the same because the OSC and OSCM models have the same parameter (λ_{max}) in estimating g_s on soybean (Jarvis: a, e, i; BBL: b, f, j; OSC: c, g, k; OSCM: d, h, l).

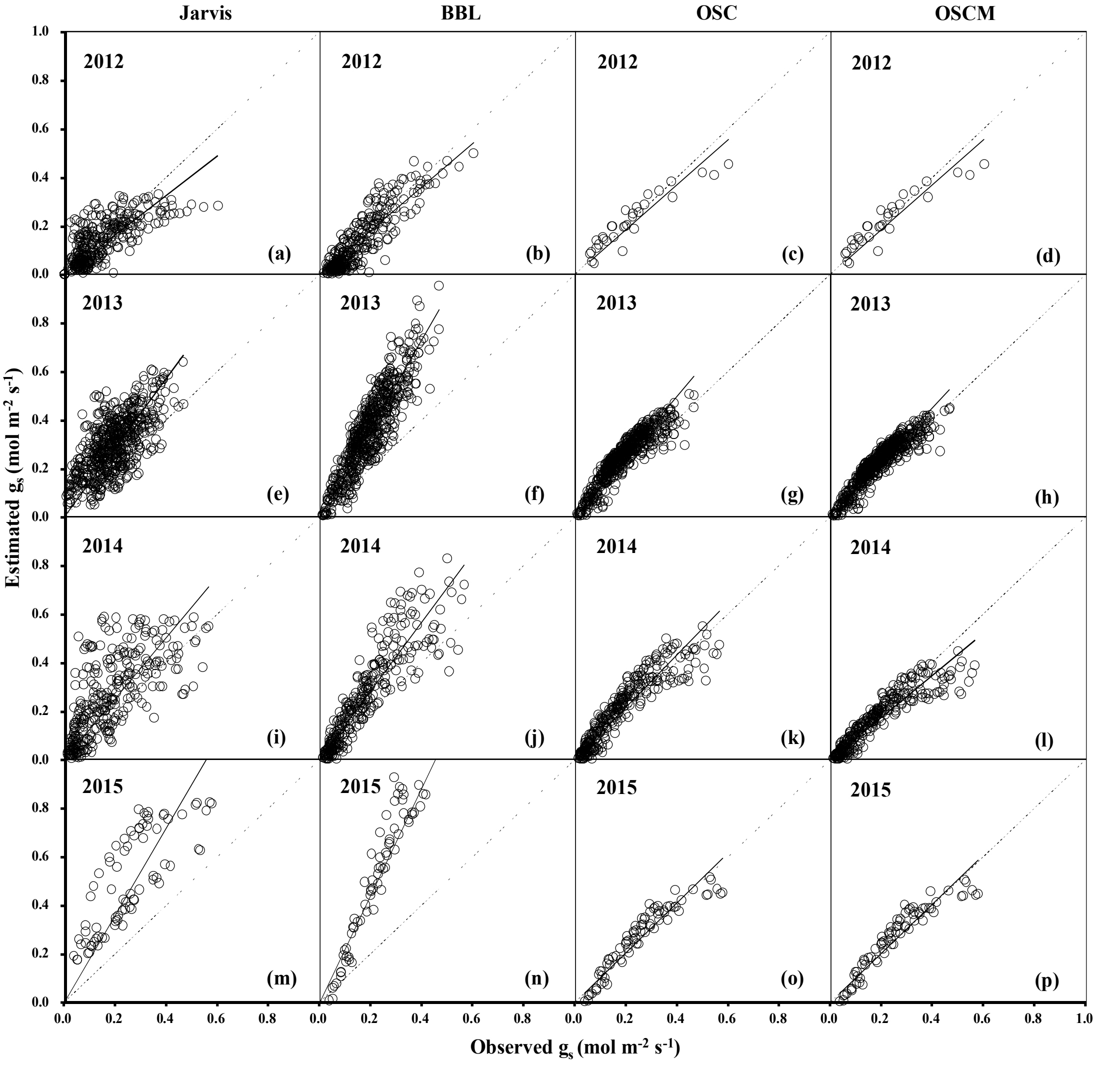

Figure 2. Comparison of observed and estimated stomatal conductance (g_s) by four models for maize in 2012, 2013, 2014, 2015. Calibration: a-d, validation: e-p, in which c and d are the same because the OSC and OSCM models have the same parameter (λ_{max}) in estimating g_s on maize (Jarvis: a, e, i, m; BBL: b, f, j, n; OSC: c, g, k, o; OSCM: d, h, l, p).

Comparison of estimated and observed stomatal conductance for soybean and maize during the whole growing seasons at different soil water contents

Residuals (estimated g_s - observed g_s) of the Jarvis and BBL models both showed a relationship with soil water content in 2012, 2013, 2015 on soybean, with simulations tending to overestimate g_s at high soil water content and underestimate g_s at low soil water content (Figure 3(a,b)). Residuals of the OSC model tended to overestimate g_s whether at high soil water content or at low soil water content (Figure 3(c)). There was little effect of soil water content on residuals of the OSCM model in 2012, 2013, 2015 on soybean, with lowest estimation error (the absolute value of residual) among the four models.

Residuals of the four models showed a similar relationship with soil water content on maize with that on soybean (Figure 4). For the Jarvis and BBL models, the simulations tended to overestimate g_s at high soil water content and underestimate g_s at low soil water content. For the OSC and OSCM models, there was little effect of soil water content on residuals. And residuals of the OSCM model were closer to 0 than the OSC model. So whatever at high or low soil water content, the OSCM model performed best with lowest estimation error among the four models.

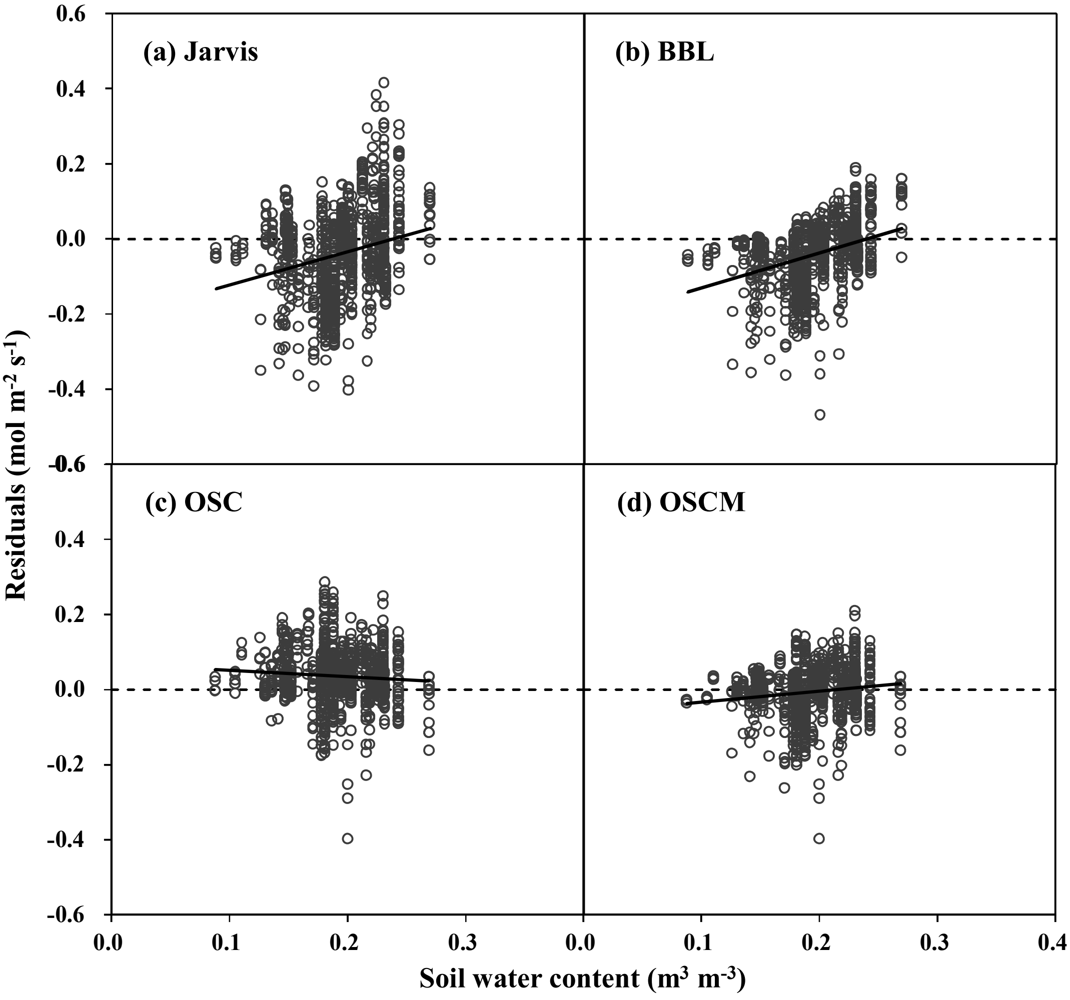

Figure 3. Residuals (estimated stomatal conductance (g_s) - observed g_s) of the four models as a function of soil water content in 2012, 2013, 2015 on soybean.

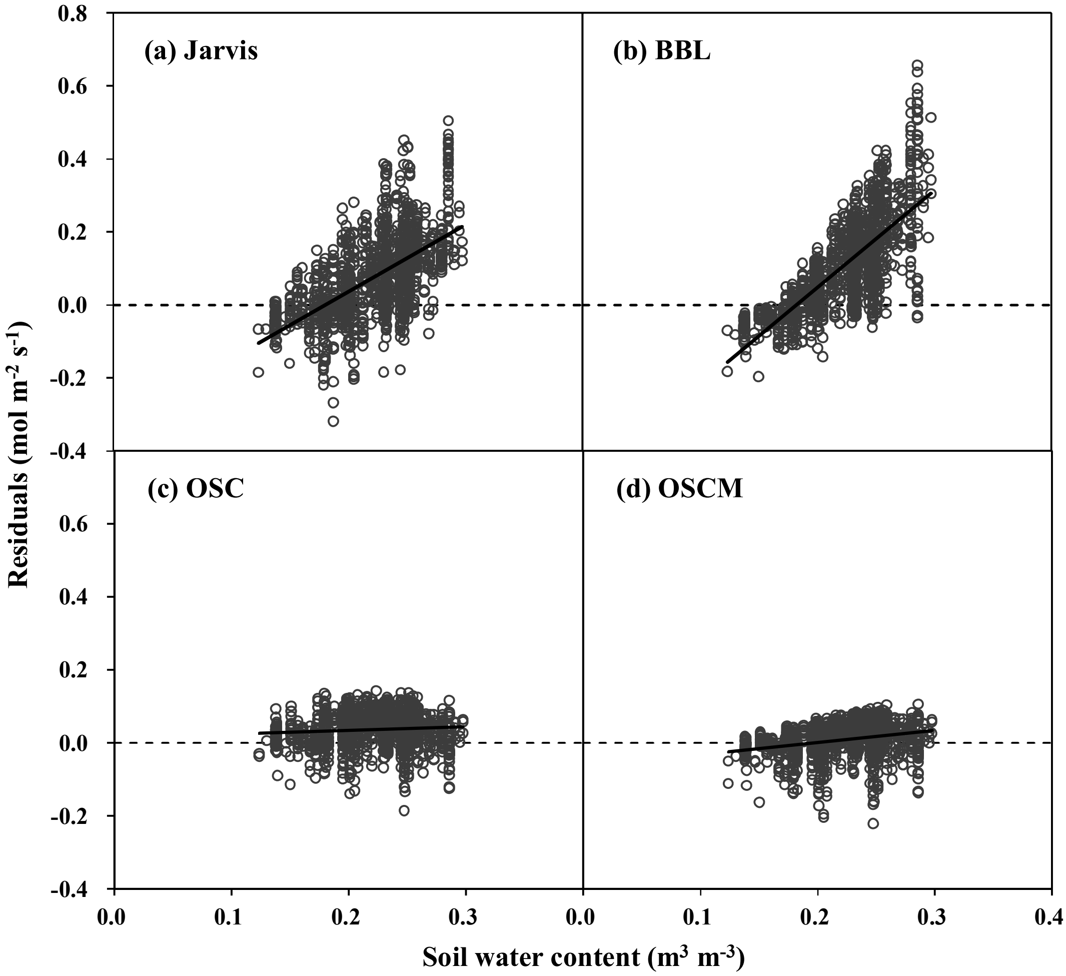

Figure 4. Residuals (estimated stomatal conductance (g_S) - observed g_S) of the four models as a function of soil water content in 2012, 2013, 2014, 2015 on maize.

Comparison of diurnal change of estimated and observed stomatal conductance for soybean and maize at different soil water contents

Comparison of estimated and measured g_S for soybean under different soil water conditions is shown as Figure 5. Whether under severe water-stressed condition (θ_V=0.14 m^3 m^{-3}) or mild water-stressed condition (θ_V=0.20 m^3 m^{-3}), diurnal change of g_S for soybean shows that g_S increased to a maximum firstly and then decreased gradually (Figure 5). Maximal g_S occurred at about 11:00 am under the mild water-stressed condition, while it occurred at 8:00 am under the severe water-stressed condition to avoid high transpiration in the midday. The trends of estimated g_S by four models were basically the same, whether water deficit was mild or severe. The OSC model overestimated g_S significantly and the BBL model underestimated it significantly, but the OSCM model estimated it accurately. When g_S decreased to the minimal values (less than about 0.03 mol m^{-2} s^{-1}) after the first peak, the estimated g_S by the four models were close to the measured value. At the second peak (Figure 5 (a)) in the afternoon, the g_S estimated by the BBL and OSCM models was close to the measured value, while the

Jarvis and OSC models overestimated g_s. So under severe water-stressed condition, the diurnal change of g_s in soybean estimated by four models was different only during 7: 00-9: 00 and 14: 00-16: 00 around the peak. But under mild water-stressed condition, the diurnal change of g_s estimated by four models was apparently different during 8: 00-17: 00. In short, for the diurnal change of g_s for soybean, whether under the mild or severe water-stressed condition, only the OSCM model estimated g_s accurately.

Comparison of diurnal change of estimated and measured g_s for maize under well-watered and water-stressed conditions is shown in Figure 6 (a) and (b). Similar to diurnal change of g_s for soybean, the diurnal change of g_s for maize estimated by the models was basically consistent with that of observed g_s except the Jarvis model. Under well-watered condition, there was obvious difference among diurnal change of g_s estimated by the four models, that BBL and Jarvis models overestimated g_s significantly while the OSC and OSCM model estimated it well. Under water-stressed condition, the BBL and Jarvis models estimated the diurnal change of g_s with large error and the OSC model overestimated it, but the OSCM model gave the close estimation to the observed values. In short, for the diurnal change of g_s estimated by four models for soybean and maize, the modified optimal models (OSCM) had the highest accuracy.

The two optimal models (OSC and OSCM) showed good consistency in estimating g_s of 2012, 2013 and 2015 for soybean and 2012, 2013, 2014 and 2015 for maize and were better than Jarvis and BBL models. That is mainly because the two optimal models are derived based on optimal stomatal regulation theory and no empirical method involved during the process of derivation. So the optimal models have strong physiologically mechanistic foundation, while the BBL model is still essentially empirical although it has considered some stomatal responses to environmental factors and the Jarvis model does not take the interactive effects between environmental factors into account. The optimal models only have one parameter-the maximum marginal water cost of carbon gain (λ_{max}). λ_{max} represents the maximum available water of plant itself in relation to plant functional type that means plant water-use-strategy and is stable at longer time scales (Katul et al., 2010; Medlyn et al., 2011; De Kauwe et al., 2015; Lin et al., 2015). And it can be obtained only using gas exchange data under well-watered condition. However, the parameters in the Jarvis and BBL models have lacking of clear biological meaning and are not stable among years due to easily affected by environmental conditions and need more data for calibration.

Among the four models, the OSCM model performed best, which improved the estimation accuracy of g_s by 7%, 12%, 13% and 6%, 36%, 58% and reduced the RMSE by 21%, 51%, 29% and 17%, 61%, 57%, for soybean and maize on average respectively. Among the two optimal models, the OSC model without considering water stress overestimated g_s for soybean and maize under water-stressed condition on short (temporal or daily) and longer (whole growing season) time scales, while performed well under well-watered condition. Therefore the OSCM models performed better than the OSC model in estimating g_s of soybean and maize under water-stressed condition. The OSCM model performed well in estimating g_s for soybean and maize at long time scale (growing period) or short time scale (temporal or daily), which proves the assumption of $f_5(\theta_v)$ in the OSCM model is rational.

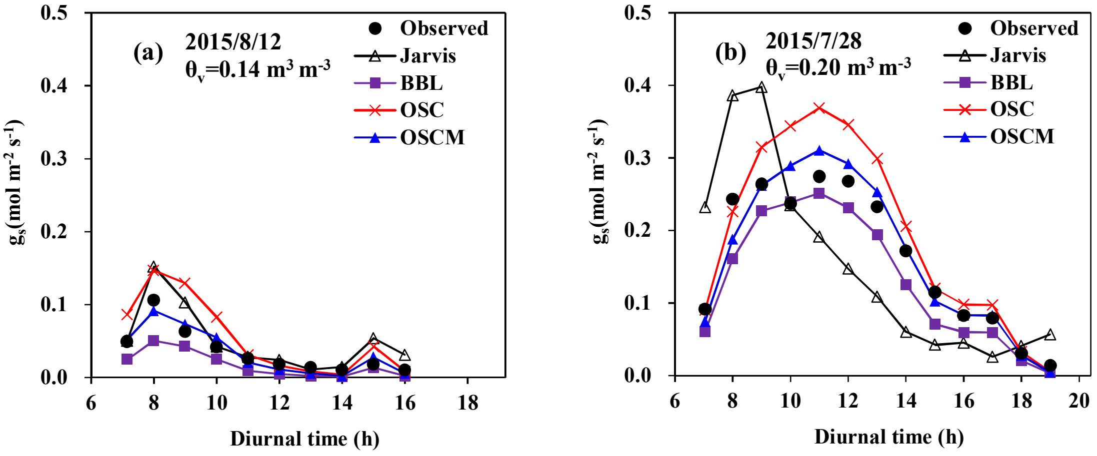

Figure 5. Comparison of diurnal change of observed and estimated stomatal conductance (g_s) by four models on soybean (a) under the severe water-stressed condition, (b) under the mild water-stressed condition.

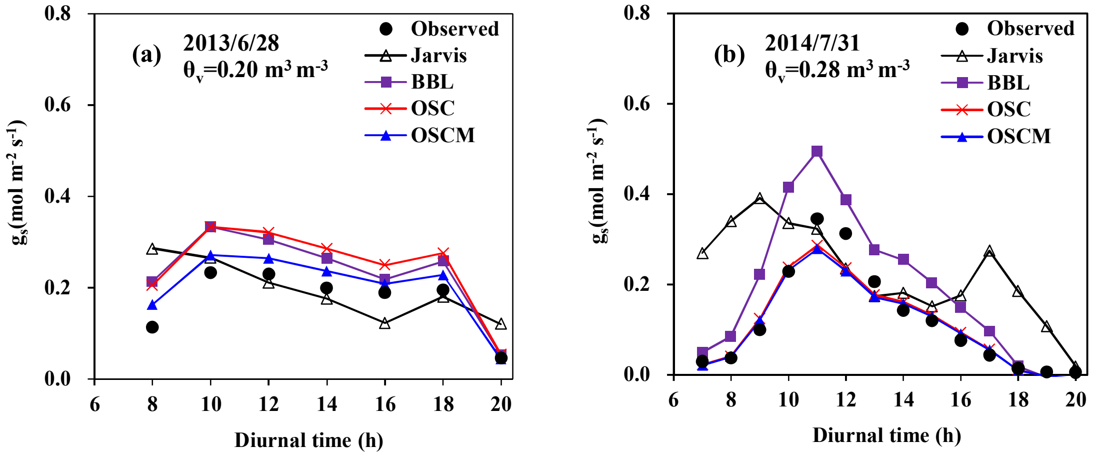

Figure 6. Comparison of diurnal change of observed and estimated stomatal conductance (g_s) by four models on maize (a) under the severe water-stressed condition, (b) under the well-watered condition.

Conclusions

This study established modified optimal stomatal conductance model (OSCM) under water-stressed condition based on the optimal stomatal conductance model (OSC) by considering the relationship between marginal water cost of carbon gain (λ) and soil water content (θ_v). And it improved the estimation accuracy of stomatal conductance at leaf level for soybean and maize. The parameters in the OSCM and OSC models were less than those of the Jarvis and BBL models, but the estimation accuracy was higher. For estimating stomatal conductance on soybean and maize among different years, the two optimal models performed more stable than the Jarvis and BBL models. And the estimation accuracy of g_s on soybean and maize by the OSCM model considering water stress were the highest, which was improved by 7%, 25% and 35% if compared with the OSC, Jarvis and BBL models on average. For the diurnal change of g_s on soybean and maize, the estimated g_s by the OSCM model was more accurate than that by Jarvis and BBL models whether under water-stressed condition or not, while the OSC model estimated g_s accurately under well-watered condition while overestimated it under water-stressed condition. Thus under water-stressed condition, the OSCM model is recommended due to its high accuracy and simple form. Therefore, the OSCM model, as a mechanical stomatal conductance model, can be applied in the carbon and water cycles at different spatial scales in the arid area where drought stress is a major factor.

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