Modeling the water use efficiency of soybean and maize plants under environmental stresses: application of a synthetic model of photosynthesis-transpiration based on stomatal behavior

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Summary

Understanding the variability of plant WUE and its control mechanism can promote the comprehension to the coupling relationship of water and carbon cycle in terrestrial ecosystem, which is the foundation for developing water-carbon coupling cycle model. In this paper, we made clear the differences of net assimilation rate, transpiration rate, and WUE between the two species by comparing the experiment data of soybean (Glycine max Merr.) and maize (Zea mays L.) plants under water and soil nutrient stresses. WUE of maize was about two and a half times more than that of soybean in the same weather conditions. Enhancement of water stresses led to the marked decrease of $A_m$ and $E_m$ of two species, but water stresses of some degree could improve WUE, and this effect was more obvious for soybean. WUE of the two species changed with $\Psi_L$ in a second-order curve relation, and the WUE at high fertilization was higher than that at low fertilization, this effect was especially obvious for maize. Moreover, according to the synthetic model of photosynthesis-transpiration based on stomatal behavior (SMPTS) presented by Yu et al. (2001), the WUE model and its applicability were discussed with the data measured in this experiment. The WUE estimated by means of the model accorded well with the measured values. However, this model underestimated the WUE for maize slightly, thus further improvement on the original model was made in this study. Finally, by discussing some physiological factors controlling $A_m$ and WUE, we made clear the physiological explanation for differences of the relative contributions of stomata- and mesophyll processes to control of $A_m$ and WUE, and the applicability of WUE model between the two species. Because the requirement to stomatal conductance by unit change of net assimilation rate is different, the responses of opening-closing activity of stomata to environmental stresses are different between the two species. To obtain the same level of net assimilation rate, soybean has to open its stomata more widely to keep small stomatal resistance, as compared with maize.

Key words: environmental stresses – maize (Zea mays L.) – soybean (Glycine max Merr.) – water use efficiency (WUE)
Abbreviations: $A_m$ = net assimilation rate of CO$_2$ (µmol m$^{-2}$ s$^{-1}$). – $C_a =$ ambient CO$_2$ concentration (µmol mol$^{-1}$). – $C_i =$ intercellular CO$_2$ concentration (µmol mol$^{-1}$). – $C_o =$ CO$_2$ concentration at the leaf surface (µmol mol$^{-1}$). – $D_s =$ saturation deficit (hPa). – $e_a =$ water vapor pressure of air (hPa). – $e_{aT}(T_L) =$ saturated water vapor pressure at leaf temperature (hPa). – $E_m =$ transpiration rate (mol m$^{-2}$ s$^{-1}$). – $g_{c} =$ internal conductance to CO$_2$ (mol m$^{-2}$ s$^{-1}$). – $g_{c}^{m} =$ internal conductance for maize (mol m$^{-2}$ s$^{-1}$). – $g_{c}^{s} =$ internal conductance to soybean (mol m$^{-2}$ s$^{-1}$). – $g_{sc} =$ stomatal conductance to CO$_2$ (mol m$^{-2}$ s$^{-1}$). – $g_{sc,max} =$ the maximum of stomatal conductance to CO$_2$ (mol m$^{-2}$ s$^{-1}$). – $g_{sw} =$ stomatal conductance to water (mol m$^{-2}$ s$^{-1}$). – $P =$ atmospheric pressure (hPa). – $Q_p =$ photosynthetic photon flux density (µmol m$^{-2}$ s$^{-1}$). – $R_{cs} =$ relative contribution of stomatal processes to CO$_2$ assimilation. – $R_{c3} =$ relative contribution of internal processes to CO$_2$ assimilation. – $RH =$ relative humidity (%). – $f_{bw} =$ boundary layer resistance to H$_2$O and to CO$_2$ (m$^2$ s$^{-1}$ mol$^{-1}$). – $r_{sc} =$ total resistance for gas-phase diffusion of CO$_2$ (m$^2$ s$^{-1}$ mol$^{-1}$). – $r_e =$ internal resistance to CO$_2$ (m$^2$ s$^{-1}$ mol$^{-1}$). – $r_{sc} =$ stomatal resistance to CO$_2$ (m$^2$ s$^{-1}$ mol$^{-1}$). – $f_{bw}, f_{ic} =$ total resistance to fluxes of H$_2$O and CO$_2$ for leaves (m$^2$ s$^{-1}$ mol$^{-1}$). – $T_L =$ leaf temperature (°C). – $WUE =$ water use efficiency. – $WUE_c =$ modified WUE. – $\Gamma =$ CO$_2$ compensation point with dark respiration (µmol mol$^{-1}$). – $\Gamma_c =$ CO$_2$ compensation point without dark respiration (µmol mol$^{-1}$). – $\Gamma_{C_3} =$ CO$_2$ compensation point of C$_3$ plants (µmol mol$^{-1}$). – $\Gamma_{C_4} =$ CO$_2$ compensation point of C$_4$ plants (µmol mol$^{-1}$). – $\Psi_L =$ leaf water potential (MPa)

Introduction

Water use efficiency (WUE) of plants is an important parameter in evaluating agriculture productivity and planning water resource utilization in semi-arid and arid regions. More importantly, understanding the variability of plant WUE and its control mechanism can promote the comprehension to the coupling relationship of water and carbon cycle, which is the foundation for developing a water-carbon coupling cycle model in ecosystem. Photosynthesis and transpiration are controlled by the identical stomata simultaneously, so the knowledge of biological mechanism for diffusion processes of water vapor and CO$_2$ controlled by stomatal behavior may be the foundation for determining WUE. Based on this, we think that developing synthetic model based on the comprehensive understanding to physiological mechanism of photosynthesis and transpiration controlled by stomatal behavior is an efficient approach for modeling the WUE (Yu et al. 2001, 2003). A simple model based on leaf gas-exchange was developed by Bierhuizen and Slatyer (1956), and had been discussed in more detail by Fischer and Turner (1978), Nobal (1980) and Jones (1992). Moreover, Jones (1976), Cowan (1977), von Caemmerer and Farquhar (1981) presented more sophisticated leaf models, which included more complete description of leaf photosynthesis and energy balance. Cowan (1977), Cowan and Farquhar (1977) developed a model to quantify the optimal behavior for stomata in a changing environment.

In recent studies, a semi-empirical relationship between net assimilation rate of CO$_2$, $A_m$, and stomatal conductance, $g_{sc}$, was first proposed by Ball et al. (1987), and its modified versions were proposed by Lloyd (1991), Collatz et al. (1991) and Leuning (1990, 1995). The empirical relationship has been widely used at scales from individual leaves (Leuning 1990, 1995, Tenhunen et al. 1990, Collatz et al. 1991, Harley et al. 1992), canopies (Hatton et al. 1992), landscapes (McMurtrie et al. 1992), to global (Sellers et al. 1992, 1996, Woodward and Smith 1994). On the other hand, a biochemical model for estimating the net assimilation rate of CO$_2$ was first presented by Farquhar et al. (1980), and following this many researchers have tried to improve and apply this model to C$_3$ (von Caemmerer and Farquhar 1981, Brooks and Farquhar 1985, Harley et al. 1985, 1992, McMurtrie et al. 1992, Leuning 1995) and C$_4$ plants (Collatz et al. 1991, 1992). Besides, for C$_3$ plants, Leuning (1995) presented a combined stomatal-photosynthesis model that combines stomatal conductance model with a photosynthesis biochemical model.

The above-mentioned studies provide us with a very useful approach for understanding the WUE through photosynthesis and transpiration models. However, too many parameters involved in estimating the photosynthesis make it difficult to put the model into practical use. Yu et al. (2001) developed a synthetic model of photosynthesis-transpiration based on stomatal behavior (SMPTSB) in a different way. It was ready for practical use, and the result showed that the model could be used effectively to estimate transpiration, photosynthesis, and WUE of maize and soybean without environmental stresses. However, applicability of the model under environmental stresses has not been examined. In this study, we discussed the effects of soil water and nutrient stresses on WUE of soybean and maize plants, and examined the modeling of WUE under environmental stresses and the applicability of WUE model. Moreover, by discussing some physiological factors controlling $A_m$ and WUE, we made clear the physiological explanation for the differences of the relative contributions of stomata- and mesophyll processes to control of $A_m$ and WUE, and the applicability of WUE model between the two species.
Models

Synthetic model of photosynthesis-transpiration

Yu et al. (2001) presented a synthetic model for estimating photosynthesis and transpiration based on stomatal behavior (SMPTSB). In this model, the estimation equation for CO₂ assimilation, \( A_m \), is given as

\[
A_m = \frac{(C_a - \Gamma_s) - 1.56(C_a - \Gamma)(a_1 f(D_s))}{1.37 r_{bw} + r_c}
\]

(1)

where, \( C_a \) is ambient CO₂ concentration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( \Gamma_s \) is CO₂ compensation point without dark respiration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( \Gamma \) is CO₂ compensation point with dark respiration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( r_{bw} \) is boundary layer resistance to \( \text{H}_2\text{O} \) (\( \text{m}^2 \text{s}^{-1} \text{mol}^{-1} \)), \( r_c \) is defined as internal resistance (\( \text{m}^2 \text{s}^{-1} \text{mol}^{-1} \)), \( a_1 \) is coefficient, \( f(D_s) \) represents response functions of stomatal conductance, \( g_{sw} \) (\( \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), to humidity at the leaf surface, the term \( a_1 f(D_s) \) has no unit.

As the basis of sub-models of evapotranspiration and photosynthesis, the model of stomatal conductance is of great importance. Leuning (1995) presents a stomatal conductance model

\[
g_{sw} = g_0 + a_1 A_m f(D_s)(C_a - \Gamma)
\]

(2)

where \( C_a \) is ambient CO₂ concentration at the leaf surface (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( g_0 \) is residual stomatal conductance (as \( A_m \rightarrow 0 \) when \( Q_p \rightarrow 0 \)). Note that \( g_{sw} \) is not defined by this equation when \( C_a = \Gamma \) (Leuning 1995).

Because the estimation error of the photosynthesis arising from the difference between \( \Gamma_s \) and \( \Gamma \) was not significant (Yu et al. 2001), Eq. (1) can be simplified as

\[
A_m = \frac{(C_a - \Gamma_s)(1 - 1.56(a_1 f(D_s)))}{1.37 r_{bw} + r_c}
\]

(3)

The transpiration rate, \( E_m \) (\( \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), is described as follow

\[
E_m = \frac{(e_{sw}(T_s) - e_a)P}{r_{bw} + (a_1 f(D_s) - 1.56)(1.37 r_{bw} + r_c)}
\]

(4)

where \( e_{sw}(T_s) \) is water vapor pressure in the stomata cavity (hPa), usually approximated by saturated water vapor pressure at leaf temperature (\( T_s \)), \( e_a \) is water vapor pressure of air (hPa), \( P \) is atmospheric pressure (1013 hPa).

Water use efficiency models

Water use efficiency (WUE) is defined as the ratio of \( A_m \) to \( E_m \) in \( \mu \text{mol} \text{CO}_2 \text{mol}^{-1} \text{H}_2\text{O} \). By combining Eq. (1) with Eq. (4), the WUE model is obtained as

\[
\text{WUE} = \frac{(C_a - \Gamma_s)(1 - 1.56(a_1 f(D_s)))}{(e_{sw}(T_s) - e_a)P} K_v
\]

(5)

where \( K_v \), a term related to the \( r_{bw} \), \( r_c \), and \( f(D_s) \), can be described as

\[
K_v = \frac{\frac{r_{bw}}{1.37 r_{bw} + r_c} + \frac{1}{g_0 (1.37 r_{bw} + r_c) + a_1 f(D_s) - 1.56}}{g_0 (1.37 r_{bw} + r_c)}
\]

(6)

Furthermore, if Eq. (3) is combined with Eq. (4), a simplified model of WUE can be gotten as

\[
\text{WUE} = \frac{(C_a - \Gamma_s)(1 - 1.56(a_1 f(D_s)))}{(e_{sw}(T_s) - e_a)P} K_v
\]

(7)

In view that dry matter yield is often of concern in agronomic studies, it is more popular to express equations in terms of mass fluxes of CO₂ (WUE, mg CO₂ g⁻¹ H₂O),

\[
\text{WUE} = \frac{M_r \times 10^{-3} A_m}{M_w E_m} = \frac{44}{18000} \frac{A_m}{E_m}
\]

(8)

Materials and Methods

Field experimental site

The investigation was conducted in the summer of 1998 in the experimental field of the Faculty of Horticulture, Chiba University, located in Matsudo (35° 46′ N, 139° 54′ E), Japan. In the end of June in 1998, soybean (Glycine max Merr., cv. Sayamusume) and maize (Zea mays L., cv. Haniebantamu) were sawn to pots (diameter 0.16 m, height 0.19 m, area 1/50 m²). On July 24th, fertilizer (888 compound fertilizer, 8 % NH₄-N, 8 % soluble P₂O₅, 8 % soluble K₂O) was added to the pots.

The amount of fertilizer applied was designed into three levels: lower (F₀, 0 g pot⁻¹), medium (F₁, 3.0 g pot⁻¹), and higher (F₂, 9 g pot⁻¹), equivalent to 0, 120, and 360 kg ha⁻¹ of N, P₂O₅ and K₂O, respectively. Additionally, in August, by weighing pots with electronic scale, six levels of moisture stresses from field capacity (W1) to plant wilting point (W6) were imposed on the plants with specific level of fertilization treatments. The plants in the 18 pots treated by combining water stresses with fertilization treatment for each crop were investigated under the research objectives.

Measurement of net assimilation rate, transpiration rate, and stomatal conductance

Net assimilation rate, \( A_m \), transpiration rate, \( E_m \), and stomatal conductance, \( g_{sw} \), were measured by means of portable photosynthesis system (LI-6200, LI-COR.). The measurements were performed twice in the morning and in the afternoon on August 21st and 22nd of 1998 for maize and soybean, in the order of water stress degree for each fertilization treatment. The site of measurement was at the center of the leaf surface at two different leaf positions, i.e., on the 2nd and 4th leaf from the top of the plants. The sampling protocol for these measurements involved first measuring these items of the 2nd leaf surface from the first pot to the 18th pot, and subsequently the same measurements for the 4th leaf surface were conducted from the 18th pot to the first pot. Average values measured twice at the 2nd and 4th leaf were used in the analysis.

Observation of environmental variables

Leaf temperature, \( T_s \) (°C), saturation deficit, \( D_s \) (hPa), and photosynthetic photon flux density, \( Q_p \) (\( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), were also recorded by
means of sensors attached to the photosynthesis system, at the same time as the above measurement. Mean values of these environmental variables measured twice at the 2nd and 4th leaf were used in result analysis. Soil water content was calculated according to the weight of pot and dry soil in it. Simultaneously, using a pressure chamber (Model 3005, SMEC), measurements of leaf water potential, $\Psi_L$ (MPa), were performed twice in the morning and in the afternoon only on 21st for soybean and only on 22nd for maize in August of 1998. By sampling two sheets of leaves from each pot in which maize grew, water potentials of about 1/3 part from leaf tip and the middle part of the leaf were measured. For soybean, two sheets of leaflet of each two compound leaves were taken for measuring leaf water potential. In the analysis, we used mean values measured four times for each pot.

**Model evaluation**

Values of the parameters in the model were calculated by linear or non-linear least square method, and their adaptabilities were evaluated with $R^2$, Sl, RMSE and RRMSE. $R^2$ is the coefficient of determination of the regression formula for the model. Sl is the slope of the linear regression curve established between the measured values and the values estimated by means of the model. RMSE and RRMSE are root mean square error and relative root mean square error, respectively, and calculated by

$$
RMSE = \left[ \frac{1}{n-1} \sum (Y_{\text{est}} - Y_{\text{mea}})^2 \right]^{1/2}
$$

$$
RRMSE = 100 \ \text{RMSE}/\bar{Y}_{\text{mea}}
$$

where $n$ is the number of data, $Y_{\text{est}}$ represents the estimated value, and $Y_{\text{mea}}$ are the measured value and their mean value, respectively.

**Results**

**Effects of soil water and nutrient stresses on water use efficiency**

Figure 1 shows the changes of soil water content in pots and leaf water potential of the plants grown in the pots. For water stresses of the same level, soil water content in the pot grown maize had no obvious difference from that grown soybean.

<table>
<thead>
<tr>
<th></th>
<th>$A_m$ (µmol m$^{-2}$ s$^{-1}$)</th>
<th>$E_m$ (mmol m$^{-2}$ s$^{-1}$)</th>
<th>WUE (mg g$^{-1}$)</th>
<th>$Q_p$</th>
<th>$T_a$ (°C)</th>
<th>$C_a$ (µmol mol$^{-1}$)</th>
<th>RH (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soybean Minimum</td>
<td>0.15</td>
<td>0.328</td>
<td>0.066</td>
<td>207.3</td>
<td>32.9</td>
<td>318.9</td>
<td>42.5</td>
</tr>
<tr>
<td>Maximum</td>
<td>33.11</td>
<td>17.168</td>
<td>8.761</td>
<td>1414.0</td>
<td>40.7</td>
<td>401.3</td>
<td>84.1</td>
</tr>
<tr>
<td>Averages</td>
<td>15.39</td>
<td>8.768</td>
<td>4.391</td>
<td>817.7</td>
<td>37.2</td>
<td>349.1</td>
<td>71.2</td>
</tr>
<tr>
<td>Maize Minimum</td>
<td>1.54</td>
<td>2.663</td>
<td>1.214</td>
<td>392.4</td>
<td>34.5</td>
<td>280.9</td>
<td>49.9</td>
</tr>
<tr>
<td>Maximum</td>
<td>31.48</td>
<td>7.194</td>
<td>21.197</td>
<td>1461.0</td>
<td>41.1</td>
<td>405.3</td>
<td>80.3</td>
</tr>
<tr>
<td>Averages</td>
<td>17.46</td>
<td>4.158</td>
<td>10.773</td>
<td>812.4</td>
<td>36.8</td>
<td>339.2</td>
<td>69.5</td>
</tr>
</tbody>
</table>

$Q_p$ is photosynthetic photon flux (µmol m$^{-2}$ s$^{-1}$), $T_a$ is air temperature (°C), $C_a$ is ambient CO$_2$ concentration (µmol mol$^{-1}$), and RH is relative humidity (%).

![Figure 1](image-url)
While leaf water potentials, $\Psi_L$ of soybean were significantly lower than those of maize for all levels of water stresses.

Table 1 shows minimum, maximum and averages of $A_m$, $E_m$ and WUE of soybean and maize, as well as weather conditions in four measurements. Figure 2 shows the changes of $A_m$, $E_m$ and WUE of the two species under water and nutrient stresses. From Table 1 and Figure 2, we found that, under similar conditions, $A_m$ of maize was a little higher than that of soybean, but $E_m$ of maize was obviously lower than that of soybean, only one-half as much as that of soybean, thereby, WUE of maize (average 10.773 mg g$^{-1}$) was markedly higher than that of soybean (average 4.391 mg g$^{-1}$), about two and a half times as much as that of soybean. In addition, although fertilization treatment had a little effect on $A_m$, $E_m$ and WUE of soybean, $A_m$ of maize increased with the amount of fertilizer applied and its WUE increased obviously (Fig. 2 and Table 2).

Water stresses had evident effects on $A_m$ and $E_m$ of the two plants, enhancement of water stresses led to the marked decrease of $A_m$ and $E_m$, but water stresses of some degree could improve WUE, and this effect was more obvious for soybean (Fig. 2).

Figures 3A and B show relationships between leaf water potential, $\Psi_L$, and $A_m$, $E_m$, as well as WUE. Obviously, $A_m$, $E_m$, and WUE decreased with $\Psi_L$, but the dropping patterns were different from each other. Generally, due to $E_m$ of both species decreased exponentially with $\Psi_L$, slopes of curves became large when leaves were in higher water potential range ($\approx 0.7$ MPa for maize and $> 1.0$ MPa for soybean). Conversely, when leaves were in higher water potential range, $A_m$ of soybean decreased with a small slope of curves, while $A_m$ of maize increased to some degree. As a result, WUE, as the ratio of $A_m$ to $E_m$, changed with $\Psi_L$ in a second-order curve. This implied that some degree of water stress from soil was helpful to the promotion of WUE (Fig. 2, Fig. 3A and B). Undoubtedly, this is very important to the productivity of water-saving agriculture in semi-arid and arid regions. When WUE reached maximum, $\Psi_L$ of soybean and maize were about $-0.9$ and $-0.7$ MPa, respectively, the corresponding soil volumetric water content was about 35–37 m$^3$ m$^{-3}$.

Relationships between $\Psi_L$ and $g_{sw}$, as well as $g_{ic}$ were plotted in Figures 3C and D. It can be found that the relationship of $\Psi_L$ with $g_{sw}$ was similar to that with $A_m$, while the relationship of $\Psi_L$ with $g_{ic}$ was similar to that with $E_m$. This suggested that changes of $g_{sw}$ and $g_{ic}$ became small, and in turn, $A_m$ and $E_m$ were regulated, as $\Psi_L$ of the leaves under water stresses decreased. Besides, Table 2 compared the averages of $A_m$, $E_m$, WUE, $g_{sw}$, and $g_{ic}$ of the two species under each fertilization treatments. A general trend was that $A_m$ and WUE of both species increased with the amount of fertilizer applied, but maize had a more significant response, as compared with soybean (Table 2). This may be due to a larger fertilizer requirement for maize as compared with soybean,
Figure 3. Relationships between leaf water potential, $\Psi_L$, and net assimilation rate, $A_m$, transpiration rate, $E_m$, as well as water use efficiency, WUE, and relationships between $\Psi_L$ and stomatal conductance, $g_{sw}$, as well as internal conductance, $g_{ic}$, in different experimental treatments.

Table 2. Comparison AVG ± STD of net assimilation rate, $A_m$, transpiration rate, $E_m$, and water use efficiency, WUE, stomatal conductance, $g_{sw}$, and internal conductance, $g_{ic}$, of soybean and maize plants for individual fertilization treatments (F0, F1 and F2). AVG is average value, and STD is standard deviation.

<table>
<thead>
<tr>
<th>Fertilization treatments</th>
<th>$A_m$ (µmol m⁻² s⁻¹)</th>
<th>$E_m$ (mmol m⁻² s⁻¹)</th>
<th>WUE (mg g⁻¹)</th>
<th>$g_{sw}$ (mol m⁻² s⁻¹)</th>
<th>$g_{ic}$ (mol m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soybean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F0</td>
<td>14.60±7.85</td>
<td>8.816±2.355</td>
<td>3.71±1.73</td>
<td>0.838±0.452</td>
<td>0.0645±0.0353</td>
</tr>
<tr>
<td>F1</td>
<td>15.11±7.70</td>
<td>8.534±2.270</td>
<td>3.96±1.78</td>
<td>0.763±0.358</td>
<td>0.0689±0.0363</td>
</tr>
<tr>
<td>F2</td>
<td>16.46±4.46</td>
<td>8.953±1.724</td>
<td>4.44±0.62</td>
<td>0.780±0.360</td>
<td>0.0747±0.0207</td>
</tr>
<tr>
<td>Maize</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F0</td>
<td>14.83±6.31</td>
<td>4.673±0.637</td>
<td>7.48±2.69</td>
<td>0.271±0.077</td>
<td>0.0652±0.0306</td>
</tr>
<tr>
<td>F1</td>
<td>17.54±6.62</td>
<td>3.884±0.419</td>
<td>10.94±1.18</td>
<td>0.236±0.059</td>
<td>0.0951±0.0239</td>
</tr>
<tr>
<td>F2</td>
<td>20.01±5.57</td>
<td>3.917±0.523</td>
<td>12.29±2.11</td>
<td>0.255±0.082</td>
<td>0.1226±0.0454</td>
</tr>
</tbody>
</table>
which suggested that suitable application of fertilizer could improve utilization efficiency of limited water resources in semi-arid and arid regions.

**Modeling stomatal conductance and internal conductance**

In the stomatal conductance model of Eq. (2), \( f(D_s) \) is a general function describing response of stomatal conductance to humidity. Numerous expressions for it had been proposed. Yu et al. (2001) found that the following forms performed better.

\[
\begin{align*}
 f_1(D_s) &= h_s \quad \text{(11.1)} \\
 f_2(D_s) &= 1 - D_s/D_0 \quad \text{(11.2)} \\
 f_3(D_s) &= (1 + D_s/D_0)^{-1} \quad \text{(11.3)}
\end{align*}
\]

Table 3. Parameters of the regression formulas of \( f(D_s) \) in the model, \( g_{sw} = g_0 + a_1 A_m f(D_s)/(C_a - \Gamma) \), for estimating stomatal conductance, and the corresponding coefficient of determinations, \( R^2 \), of the models for soybean and maize.

<table>
<thead>
<tr>
<th>( f(D_s) )</th>
<th>( g_0 )</th>
<th>( a_1 )</th>
<th>( D_0 )</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soybean</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f_1(D_s) = h_s )</td>
<td>0.070</td>
<td>0.173</td>
<td></td>
<td>0.871</td>
</tr>
<tr>
<td>( f_2(D_s) = 1 - D_s/D_0 )</td>
<td>0.064</td>
<td>19.463</td>
<td>52</td>
<td>0.882</td>
</tr>
<tr>
<td>( f_3(D_s) = (1 + D_s/D_0)^{-1} )</td>
<td>0.052</td>
<td>22.943</td>
<td>22</td>
<td>0.874</td>
</tr>
<tr>
<td>Maize</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f_1(D_s) = h_s )</td>
<td>0.116</td>
<td>0.036</td>
<td></td>
<td>0.635</td>
</tr>
<tr>
<td>( f_2(D_s) = 1 - D_s/D_0 )</td>
<td>0.117</td>
<td>3.375</td>
<td>70</td>
<td>0.627</td>
</tr>
<tr>
<td>( f_3(D_s) = (1 + D_s/D_0)^{-1} )</td>
<td>0.118</td>
<td>3.952</td>
<td>30</td>
<td>0.622</td>
</tr>
</tbody>
</table>

In this study, the saturation deficit around the leaves was used to replace \( D_s \) at the leaf surface in Eq. (11.1) to Eq. (11.3), and an objective non-linear parameter estimation method was used to Eq. (2), with \( f(D_s) \) having forms of Eq. (11.1) to Eq. (11.3). Results of the regression analysis were shown in Table 3. The value of \( g_0 \) was about 0.06 mol m\(^{-2}\) s\(^{-1}\) for soybean, and about 0.12 mol m\(^{-2}\) s\(^{-1}\) for maize. The values of \( D_0 \) in Eq. (11.2) and Eq. (11.3) were 52 hPa and 22 hPa for soybean, respectively, and 70 hPa and 30 hPa for maize, respectively. The \( R^2 \) values of the functions showed in Table 3 were significant at 0.01 levels, with no big differences exist. The \( R^2 \) value was about 0.64 for maize, and about 0.87 for soybean (Table 3). The responses of \( g_{sw} \) to \( A_m h_s/(C_a - \Gamma) \) and \( A_m/[1 + D_s/D_0](C_a - \Gamma) \) were illustrated in Figure 4 for maize and soybean.

According to Yu et al. (2001), the internal resistance, \( r_{ic} \), has a form of

\[
r_{ic} = \sqrt{g_{ic}} = (C_i - \Gamma_{ic})/A_m \quad \text{(12)}
\]

where \( C_i \) is intercellular CO\(_2\) concentration (\( \mu \text{mol mol}^{-1} \)), CO\(_2\) compensation points, \( \Gamma_{ic} \) (\( \mu \text{mol mol}^{-1} \)), is dependent on leaf temperature, and can be obtained by the following empirical second-order polynomial

\[
\Gamma_{c3} = 42.7 + 1.68 (T_L - 25) + 0.012 (T_L - 25)^2 \quad \text{(13a)}
\]

\[
\Gamma_{c4} = 0.1 \Gamma_{c3} \quad \text{(13b)}
\]

where \( \Gamma_{c3} \) is CO\(_2\) compensation point of C\(_3\) plants, \( \Gamma_{c4} \) is CO\(_2\) compensation point of C\(_4\) plants.

Additionally, to estimate the internal resistance, \( r_{ic} \), in Eq. (1) to Eq. (7) for estimating \( A_m, E_m, \) and WUE, correlation anal-
ysis between the internal conductance, $g_{ic}$, and various environmental variables was made. It was found that there are correlations between $g_{ic}$ and $Q_p$, $D_s$, and $\Psi_L$.

$$g_{ic}^s = 0.0798 + 9.806 \times 10^{-5} Q_p - 0.00244 D_s + 0.0413 \Psi_L;$$  \hspace{1cm} (14)

$$R^2 = 0.818, n = 72$$

$$g_{ic}^m = 0.1487 + 6.881 \times 10^{-5} Q_p - 0.00335 D_s + 0.0632 \Psi_L;$$  \hspace{1cm} (15)

$$R^2 = 0.542, n = 72$$

where $g_{ic}^s$ and $g_{ic}^m$ are internal conductance for soybean and maize, respectively. Two models were significant at 0.01 levels; in addition, the $R^2$ value of the model for soybean was higher than that for maize. Figure 5 shows the comparison between the values of $g_{ic}$ measured and estimated by means of the models as Eqs. (14) and (15) for soybean and maize, respectively.

Figure 5. Comparison between the values of internal conductance, $g_{ic}$, measured and estimated by means of the models as Eqs. (14) and (15) for soybean and maize, respectively.

Modeling water use efficiency

A simple model of WUE, which is based on leaf gas exchange, is obtained as

$$WUE = \frac{(C_a - C_i) \left( \frac{r_{sw} + r_{tw}}{r_{sc} + r_{tc}} \right) }{P e_{dc} (T_{cl} - e_d) P} \frac{r_{tw} + r_{tw}}{g_{ic}} \frac{(C_a - C_i)}{e_{dc} (T_{cl} - e_d) P}$$  \hspace{1cm} (16)
where \( r_{bw} \) is boundary layer resistance to \( \text{H}_2\text{O} \) (\( \text{m}^2 \text{s mol}^{-1} \)), \( r_{bc} \) and \( r_{sc} \) are boundary layer resistance and stomatal resistance (\( \text{m}^2 \text{s mol}^{-1} \)) to \( \text{CO}_2 \), respectively. \( r_{gc} = r_{bc} + r_{sc} \) and \( r_{tw} = r_{bw} + r_{sw} \), where \( r_{gc} \) is total resistance for gas-phase diffusion of \( \text{CO}_2 \) from atmosphere to the stomata cavity (\( \text{m}^2 \text{s mol}^{-1} \)), \( r_{tw} \) is total resistance to \( \text{H}_2\text{O} \) (\( \text{m}^2 \text{s mol}^{-1} \)). Because \( \frac{r_{bc} + r_{sc}}{H} \leq 1.56 \frac{r_{bw} + r_{sw}}{H} \), Eq. (16) can be simplified as

\[
\text{WUE} = \frac{C_c - \Gamma_*}{1.56 \left( \frac{r_{tw}}{r_{tc}} \right)} / P
\]

where \( C_c / C_a \) is usually assumed as a constant dependent on species. On the other hand, the WUE model can be expressed in another form as

\[
\text{WUE} = \frac{(C_c - \Gamma_*)}{(e_w(T_L) - e_a)P} \cdot \frac{r_{tw}}{r_{bc} + r_{sc} + r_{tc}} = \frac{r_{tw}}{r_{bc} + r_{sc} + r_{tc}} \left( C_c - \Gamma_* \right) / P
\]

with \( r_{tc} = r_{bc} + r_{sc} + r_{ic} \) and \( \Gamma_* \) is assumed as a constant. According to Eq. (17) and (18), the relation between \( C_c / C_a \) and \( \frac{r_{tw}}{r_{tc}} \) can be described as

\[
\frac{r_{tw}}{r_{tc}} = \frac{1 - C_c}{C_a - \Gamma_*} \frac{C_c}{1.56 \left( C_c - \Gamma_* \right)} \left( 1 - \frac{C_c}{C_a} \right)
\]

in the case of \( \Gamma_* \ll C_c \), a linear relationship exists between \( C_c / C_a \) and \( \frac{r_{tw}}{r_{tc}} \) (Fig. 6C).

From Eq. (17) and Eq. (18), it can be understood that \( C_c / C_a \) and \( \frac{r_{tw}}{r_{tc}} \) were critical physiological parameters in determining WUE. Once either \( C_c / C_a \) or \( \frac{r_{tw}}{r_{tc}} \) is determined, Eq. (17) or (18) will become more effective for determining WUE by leaf-air vapor pressure in different climates. The relationships between the measured WUE and \( C_c / C_a \) as well as \( \frac{r_{tw}}{r_{tc}} \) were shown in Figures 6A and B. In Figure 6, there are typically two groups of data for soybean and maize, it results from the dif-

### Table 4. Estimation precision for WUE when using Eq. (5) and Eq. (7), with different functions for \( f(D_s) \) in \( g_{sw} = a_1(A_m f(D_s))/C_s - \Gamma_* \), taking the measured values for internal conductance, \( g_{ic} \), and 2.0 mol m\(^{-2}\) s\(^{-1}\) for \( g_{bw} \).

<table>
<thead>
<tr>
<th>( f(D_s) )</th>
<th>( R^2 )</th>
<th>SI</th>
<th>RMSE</th>
<th>RRMSE</th>
<th>( R^2 )</th>
<th>SI</th>
<th>RMSE</th>
<th>RRMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soybean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f_1(D_s) = h_s )</td>
<td>0.919</td>
<td>0.969</td>
<td>0.614</td>
<td>13.99</td>
<td>0.919</td>
<td>0.966</td>
<td>0.617</td>
<td>14.01</td>
</tr>
<tr>
<td>( f_2(D_s) = 1 - D_s/D_0 )</td>
<td>0.913</td>
<td>0.938</td>
<td>0.635</td>
<td>14.43</td>
<td>0.914</td>
<td>0.936</td>
<td>0.617</td>
<td>14.53</td>
</tr>
<tr>
<td>( f_3(D_s) = (1 + D_s/D_0)^{-1} )</td>
<td>0.906</td>
<td>0.943</td>
<td>0.640</td>
<td>14.57</td>
<td>0.907</td>
<td>0.941</td>
<td>0.643</td>
<td>14.64</td>
</tr>
<tr>
<td>Maize</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f_1(D_s) = h_s )</td>
<td>0.901</td>
<td>0.787</td>
<td>2.794</td>
<td>25.93</td>
<td>0.899</td>
<td>0.771</td>
<td>2.956</td>
<td>27.43</td>
</tr>
<tr>
<td>( f_2(D_s) = 1 - D_s/D_0 )</td>
<td>0.914</td>
<td>0.849</td>
<td>2.096</td>
<td>19.45</td>
<td>0.914</td>
<td>0.835</td>
<td>2.226</td>
<td>20.67</td>
</tr>
<tr>
<td>( f_3(D_s) = (1 + D_s/D_0)^{-1} )</td>
<td>0.914</td>
<td>0.843</td>
<td>2.151</td>
<td>19.86</td>
<td>0.914</td>
<td>0.830</td>
<td>2.282</td>
<td>21.19</td>
</tr>
</tbody>
</table>

\( R^2 \) is coefficient of determination, SI is slope (b) of the equation WUE' = bWUE established between the values measured (WUE) and estimated (WUE') by means of the model, RMSE is root mean square error (mg g\(^{-1}\)) and RRMSE is relative root mean square error (%).

![Figure 7](image_url). Comparison of values of water use efficiency, WUE, measured and estimated by means of Eq. (7) for soybean (A) and maize (B). Boundary layer conductance, \( g_{bw} \), was taken to be 2.0 mol m\(^{-2}\) s\(^{-1}\) and the internal conductance, \( g_{ic} \), in (A) and (B) the measured value was used. The solid line represents a line of 1:1.
Table 5. Estimation precision for WUE when using Eq. (5) and Eq. (7), with different functions of \( f(D_s) \) in \( g_{ow} = a_1 A_m f(D_s)/(C_a-T) \), and the values of internal conductance, \( g_{ic} \), estimated by Eq. (14) and Eq. (15). All symbols are the same as those in Table 4.

<table>
<thead>
<tr>
<th>( f(D_s) )</th>
<th>Eq. (5)</th>
<th>Eq. (7)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( R^2 )</td>
<td>( S/I )</td>
</tr>
<tr>
<td>Soybean</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f_1(D_s) = h_s )</td>
<td>0.699</td>
<td>0.969</td>
</tr>
<tr>
<td>( f_2(D_s) = 1 - D_s/D_0 )</td>
<td>0.631</td>
<td>0.937</td>
</tr>
<tr>
<td>( f_3(D_s) = (1 + D_s/D_0)^{-1} )</td>
<td>0.632</td>
<td>0.942</td>
</tr>
<tr>
<td>Maize</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f_1(D_s) = h_s )</td>
<td>0.627</td>
<td>0.781</td>
</tr>
<tr>
<td>( f_2(D_s) = 1 - D_s/D_0 )</td>
<td>0.632</td>
<td>0.777</td>
</tr>
<tr>
<td>( f_3(D_s) = (1 + D_s/D_0)^{-1} )</td>
<td>0.639</td>
<td>0.773</td>
</tr>
</tbody>
</table>

Figure 8. Comparison of values of water use efficiency, WUE, measured and estimated by means of Eq. (7) for soybean (A) and maize (B). Boundary layer conductance, \( g_{bw} \), was taken to be \( 2.0 \text{ mol m}^{-2} \text{s}^{-1} \) and the internal conductance, \( g_{ic} \), the estimated values by means of the models as Eqs. (14) and (15) for soybean and maize were used, respectively. The solid line represents a line of 1:1.

With the data measured in this experiment, the WUE of soybean and maize were estimated by Eq. (5) and Eq. (7) combined with \( f_1(D_s), f_2(D_s) \) and \( f_3(D_s) \), taking the measured value for \( g_{ic} \), and \( 2.0 \text{ mol m}^{-2} \text{s}^{-1} \) for \( g_{ow} \). The estimation precision of WUE was shown in Table 4. For Eq. (7), the \( R^2 \) values were more than 0.9 for both species, the RMSE were less than 0.64 mg g\(^{-1}\) for soybean and less than 2.96 mg g\(^{-1}\) for maize, and the RRMSE were less than 14.6 % for soybean and less than 27.4 % for maize, when attempting to compare the effects of different functions of \( f(D_s) \) on the estimation precision of WUE. From Table 4, it could be found that the difference of the estimation precision between Eq. (5) and Eq. (7) was almost negligible. Thus, both Eq. (5) and Eq. (7) performed well for estimating WUE. As an example, Figures 7 A and B show comparison of the WUE measured and estimated by means of Eq. (7).

Furthermore, by incorporating Eq. (14) and Eq. (15) into Eq. (5) and Eq. (7) with the different expressions of \( f(D_s) \), the WUE of soybean and maize were estimated. The estimation precisions of these models were shown in Table 5. Comparing the results in Table 4 with those in Table 5, we found that...
Figure 9. Comparison of values of water use efficiency, WUE, measured and estimated by means of the modified formula as Eq. (20) for maize. Boundary layer conductance, $g_{bw}$, was taken to be 2.0 mol m$^{-2}$ s$^{-1}$. For the internal conductance, $g_{ic}$, in (A) the measured value was used, and in (B) the value estimated by means of the model as Eq. (15) was used. The solid line represents a line of 1:1.

The estimation precision of WUE in the case of using $g_{ic}$ model was rather lower than that in the case of using the measured values. In the case of using Eq. (7), $R^2$ values were 0.63 to 0.70 for soybean and about 0.63 for maize, the values of RMSE were less than 1.04 mg g$^{-1}$ for soybean and less than 3.71 mg g$^{-1}$ for maize. The difference of the estimation precision of WUE in the case of using Eq. (5) and Eq. (7) was almost negligible. As an example, Figures 8 A and B show comparison of WUE values measured and estimated by means of Eq. (7).

According to these results, it may be said that these models of WUE had a high enough precision to be used for estimating the WUE of soybean. While for maize, these models of WUE also had sufficient precision despite there was an underestimation for almost all values (Figs. 7, 8). The slope (b) of the equation, $WUE' = bWUE$, established between the values measured (WUE) and estimated (WUE$'$) by means of the model was about 0.75–0.84 (Tables 4 and 5). Comparison of relationship between the values measured and estimated by means of Eq. (1), Eq. (3) and Eq. (4) for $A_m$ and $E_m$ respectively revealed that the underestimation for WUE should be attributed mainly to the underestimation on $A_m$. As illustrated in Table 3, $g_0$ in Eq. (2) was about 0.05–0.07 mol m$^{-2}$ s$^{-1}$ for soybean, and about 0.11–0.12 mol m$^{-2}$ s$^{-1}$ for maize. When developing model of $A_m$, we ignored the contribution of $g_0$ to $A_m$ by assuming that $g_0$ is a cuticular conductance to H$_2$O. However, the maximum of $g_{sc}$, stomatal conductance to CO$_2$ (mol m$^{-2}$ s$^{-1}$), $g_{sc} = 1/r_{sc}$, of maize under environmental stresses was 0.45 mol m$^{-2}$ s$^{-1}$, thus the $g_0$ was approximate 20% of the maximum of $g_{sc}$. If considering the contribution of $g_0$ to $A_m$, the modified form for WUE is

$$WUE_c = WUE \left(1 + g_0/g_{sc\text{,max}} \right)$$  \hspace{1cm} (20)

WUE$'_c$ is modified WUE, $g_{sc\text{,max}}$ is the maximum of $g_{sc}$. The WUE estimated by the modified formula were shown in Figure 9. Obviously, a good estimation was made. Of course, WUE changed with the amount of fertilizer applied as shown in Table 2, but we did not consider the effects of soil nutrient stresses and the interaction between water and nutrient when developing Eq. (14) and (15) for estimating $g_{ic}$. Therefore, the estimation precision of this model in the case of using the estimated value of $g_{ic}$, was rather lower than that in the case of using the measured value of $g_{ic}$ (Figs. 7 and 8), thus more accurate estimation will depend on further experiment.

Relative contributions of stomata- and mesophyll processes to control of WUE

Net assimilation rate of plants in any particular environmental conditions is limited by both the 'supply' functions controlled by supply of CO$_2$ diffusion through stomata and the 'demand' functions controlled by bio- and photo-chemical processes in the leaf mesophyll (Jones 1992, Leuning 1990, 1995). To quantitatively evaluate the relative contributions of stomata- and mesophyll processes to the control of $A_m$ and WUE, we defined the relative contribution of stomatal processes to assimilation of CO$_2$, $R_{cs}$, as

$$R_{cs} = r_{sc}/(r_{bc} + r_{sc} + r_{ic})$$  \hspace{1cm} (21)

correction of internal processes to assimilation of CO$_2$, $R_{ci}$, as

$$R_{ci} = r_{ic}/(r_{bc} + r_{sc} + r_{ic})$$  \hspace{1cm} (22)

Figure 10 A shows relationships between $A_m$ and $R_{cs}$, as well as $R_{ci}$. Fig. 10 B shows relationships between WUE and $R_{cs}$.
as well as \( R_c \). There are typically two groups of data for soybean and maize, it mainly results from the difference of WUE of the two species, which represents the eco-physiological difference of \( C_3 \) and \( C_4 \) plants. For soybean under the experimental conditions, average values of \( R_c \) and \( R_{cs} \) were 0.847 ± 0.061 and 0.113 ± 0.047, respectively. When \( A_m < 5 \, \text{mol m}^{-2} \, \text{s}^{-1} \), the \( R_{cs} \) increased with \( A_m \), but remained almost unchanged when \( A_m \geq 5 \, \text{mol m}^{-2} \, \text{s}^{-1} \). For maize without environmental stresses, Yu et al. (2003) obtained the same result as that for soybean in this study, with the average values of \( R_{ci} \) and \( R_{cs} \) of 0.772 ± 0.099 and 0.191 ± 0.084, respectively. However, under the experimental conditions, the average values of \( R_{ci} \) and \( R_{cs} \) were 0.628 ± 0.104 and 0.344 ± 0.095, respectively. Obviously, the \( R_{cs} \) was higher than that for soybean. Moreover, as indicated in Figure 10A, the \( R_{cs} \) increased with \( A_m \) slowly to near 0.5 (i.e. \( R_{ci}/R_{cs} = 1 \)) for maize. Thus, it is understood that the contribution degree of the stomatal process to \( A_m \) was lower than that of the internal process for soybean under environmental stresses. However, for maize under environmental stresses, \( R_{cs} \) and \( R_{ci} \) changed easily. That means, the \( R_{cs} \) increased and the \( R_{ci} \) decreased as \( A_m \) increased. In the same way, we think that the changes of \( R_{cs} \) and \( R_{ci} \) play an important role in controlling WUE, because the relationships between WUE and \( R_{cs} \), as well as \( R_{ci} \), were the same as those between \( A_m \) and \( R_{cs} \) as well as \( R_{ci} \) (Fig.10B).

According to Eq. (21) and Eq. (22), we obtain the following formula

\[
\frac{r_{f_{sc}}}{r_{fc}} + \frac{r_{fc}}{r_{fc}} + \frac{r_{f_{sc}}}{r_{fc}} = R_{cs} + R_{ci} + R_{cb} = 1 \tag{23}
\]

where \( R_{cb} \) is relative contribution of boundary layer resistance to assimilation of \( CO_2 \). According to Eq. (18), \( r_{fw}/r_{fc} \) can be written as

\[
r_{fw}/r_{fc} = \frac{r_{f_{sc}}}{1.37 r_{fc} + 1.56 r_{sc}} \tag{24}
\]

\[
r_{fw}/r_{fc} = 0.73 R_{cb} + 0.64 R_{cs} = 0.64 - 0.64 R_{ci} - 0.09 R_{cb}
\]

and according to Eq. (19) and Eq. (24), \( C_i/C_a \) can be written as

\[
C_i/C_a = 1 - (0.73 R_{cb} + 0.64 R_{cs}) \frac{1.56 (C_a - \Gamma_c)}{C_a} \tag{25}
\]

From Eq. (24) and (25), it is clear that \( C_i/C_a \) and \( r_{fw}/r_{fc} \) depend on \( R_{cs} \) and \( R_{ci} \). \( C_i/C_a \) is proportional negatively to \( R_{cs} \), and positively to \( R_{ci} \), while \( r_{fw}/r_{fc} \) is proportional positively to \( R_{cs} \), but negatively to \( R_{ci} \). \( C_i/C_a \) and \( r_{fw}/r_{fc} \) are important parameters related to WUE as shown in Figures 6A and B; hence the relationships between WUE and \( R_{cs} \), as well as \( R_{ci} \), as shown in Figure 10B can be theoretically explained according to the equations from Eq. (16) to Eq. (19) and Eq. (24) and Eq. (25).

**Discussion**

It has been concluded that WUE of \( C_4 \) plants is higher than that of \( C_3 \) plants. The results in this study also support this conclusion, and in addition, this study indicates the effect of water and nutrient stresses on photosynthesis, transpiration, and WUE of soybean and maize. According to the above knowledge, we discussed the WUE model under environmental stresses on the basis of the synthetic model of photosynthesis-transpiration based on stomatal behavior (SMPT SB), and examined the applicability of the model and relative
Figure 11. Relationships between net assimilation rate, $A_m$, and stomatal conductance, $g_{sc}$, internal conductance, $g_{ic}$, as well as total conductance, $g_{tc}$, and relationships between $A_m$ and CO2 concentration drops for air-to-leaf, $C_a-C_i$, $C_i-\Gamma^*$, as well as $C_a-\Gamma^*$, respectively. Figures 11A, 11B, 11C, 11D, 11E, and 11F show the relationships between $A_m$ and $g_{sc}$, $g_{ic}$, as well as total conductance, $g_{tc}$, and between $A_m$ and CO2 concentration drops for air-to-leaf, $C_a-C_i$, $C_i-\Gamma^*$, as well as $C_a-\Gamma^*$, respectively. Figure 12 shows the relationships between $A_m$ and $C_i$, $C_i/C_a$ as well as $g_{sc}$, and between $g_{ic}$ and $C_i$, $C_i/C_a$, as well as $g_{sc}$, respectively. The symbol 0 is soybean and 0 is maize.

contributions of stomata- and mesophyll processes to control of WUE using experimental data. The results show that the model can well simulate WUE of C3 and C4 plants represented by soybean and maize, and has a broad application prospect.

A very useful graphical device for investigating the mechanism of the relationships between $A_m$, and conductance, as well as CO2 concentration drops for air-to-leaf, was introduced by Jones (1992). Yu et al. (2001) made further consideration on it using the data of maize and soybean without environmental stresses. Figure 11 shows the relationships between $A_m$, and $g_{sc}$, $g_{ic}$, as well as total conductance, $g_{tc}$, and between $A_m$ and CO2 concentration drops for air-to-leaf, $C_a-C_i$, $C_i-\Gamma^*$, as well as $C_a-\Gamma^*$, respectively. Figure 12 shows the relationships between $A_m$ and $C_i$, $C_i/C_a$ as well as $g_{sc}$, and between $g_{ic}$ and $C_i$, $C_i/C_a$, as well as $g_{sc}$, respectively. The rela-
The relationship between $A_m$, $g_{ic}$ and various factors and the difference between the two species as shown in Figures 11 and 12 were approximately the same as the results (see also Fig. 4 and Fig. 5 of Yu et al. (2001), J Plant Physiol 158: 861–874) under environmental conditions without stresses. However, when compared in detail, we found that there was some difference in the response mechanism of the two plants to environmental stresses.

The slope $\frac{\partial A_m}{\partial g_{sc}}$ and $\frac{\partial A_m}{\partial (C_a - C_i)}$ are defined as the contribution to $A_m$ of unit change of $g_{sc}$ and $C_a - C_i$, respectively. Under the experimental conditions, the slope $\frac{\partial A_m}{\partial g_{sc}}$ of the linear regression formula for maize was about 3.7 times...
as much as that for soybean, and the slope \( \partial A_m/\partial(C_a-C_i) \) of the linear regression formula for soybean was about 2.17 times as much as that for maize (Figs. 11A and B). In environmental conditions without stresses, these values were 3.37 and 1.44 times respectively (Yu et al. 2001). In addition, the slope \( \partial g_{sc}/\partial A_m \) indicates the requirement of \( g_{sc} \) by the unit change of \( A_m \). In the experimental conditions, the slope \( \partial g_{sc}/\partial A_m \) and \( \partial g_{sc}/\partial g_e \) for soybean were much bigger than those for maize (Figs. 12E and F). Although relationships as mentioned above had the same trend as those without environmental stresses, however, environmental stresses increase evidently the difference of slope \( \partial A_m/\partial g_{sc} \), \( \partial A_m/\partial (C_a-C_i) \), \( \partial g_{sc}/\partial A_m \), and \( \partial g_{sc}/\partial g_e \) between the two species.

The internal conductance, \( g_{sc} \), is determined by three factors: (1) physical diffusion of CO\(_2\) in liquid-phase from intercellular space to site of carboxylation, (2) efficiency of carboxylation, and (3) dark respiration rate (Yu et al. 2003). The efficiency of carboxylation can actually be described using the dependence of photosynthesis on light (through Rubisco regeneration) and on intercellular concentration (through Rubisco activity) (Farquhar et al. 1980, Collatz et al. 1991, and Leuning 1990, 1995). In addition, if the values of \( r_{sc} \) and \( g_e \) are constants, the slope \( \partial A_m/\partial(C_i-C_\ast) \) are equal to \(-\partial\Gamma/\partial g_{sc}\), these relationships between \( A_m \) and \( (C_i-C_\ast) \) represent photosynthetic \(-\partial\Gamma/\partial g_{sc}\) functions, and showing how \( C_i \) would fall below \( C_\ast \) as \( A_m \) increases (Jones 1992). Under the experimental conditions, relationship between \( A_m \) and \( g_{sc} \) for soybean was in a linear correlation as \( A_m = 209.47g_{sc}, R^2 = 0.965, \) for maize, it was in a rectangular hyperbola as \( A_m = 48.07g_{sc}/(0.1538 + g_{sc}), R^2 = 0.828 \) (Fig. 11C). The relationship between \( A_m \) and \( (C_i-C_\ast) \) showed a negative linear correlation for soybean as \( A_m = -0.2201(C_i-C_\ast) + 65.93, R^2 = 0.686, \) for maize as \( A_m = -0.1067(C_i-C_\ast) + 8.762, R^2 = 0.614 \) (Fig. 11D). These functions were similar to the results without environmental stresses (Yu et al. 2001), however, environmental stresses led to obvious change of slope \( \partial A_m/\partial g_{sc} \) and \( \partial A_m/\partial (C_i-C_\ast) \) of the two species, and consequently made the data form into typically two groups (Figs. 11C and D).

Finally, in this study, the average value of \( C_i \) was 294.805 ± 28.238 µmol mol\(^{-1}\) for soybean, decreased to about 250µmol mol\(^{-1}\) (Figs. 12A and B), and the average value of \( C_i/C_\ast \) was 0.843 ± 0.048, changed at near 0.76 (Figs. 12C and D). Under conditions without environmental stresses, the average values of \( C_i \) and \( C_i/C_\ast \) for soybean were 280.7 ± 30.6 µmol mol\(^{-1}\) and 0.862 ± 0.0524, respectively (Yu et al. 2001). Environmental stresses led to the decrease in the average values of \( C_i \) and the increase of the average values of \( C_i/C_\ast \). That represents the effect of water stresses on photosynthesis is mainly limited by the \(-\partial\Gamma/\partial g_{sc}\) functions of CO\(_2\) controlled by stomata behavior for soybean. In contrast, for maize, the average value of \( C_i \) was 206.05 ± 46.523 µmol mol\(^{-1}\), decreased to about 130 µmol mol\(^{-1}\) (Figs. 12A and B), and the average value of \( C_i/C_\ast \) was 0.602 ± 0.098, reduced to about 0.44 (Figs. 12C and D) in this study. Under conditions without environmental stresses, the average values of \( C_i \) and \( C_i/C_\ast \) of maize were 233.0 ± 63.7 µmol mol\(^{-1}\) and 0.720 ± 0.134, respectively (Yu et al. 2001). Obviously, environmental stresses led to the increase of the average values of \( C_i \) and \( C_i/C_\ast \), which represents the effect of water stresses on photosynthesis, is mainly limited by the \(-\partial\Gamma/\partial g_{sc}\) functions controlled by Rubisco activity or RuBP regeneration for maize.

Based on the above consideration, it is easily understood that because \( C_i \) plants are different from \( C_i \) plants in the pathway of photosynthesis, then the requirement to \( g_{sc} \) by the unit change of \( A_m \) and \( g_{sc} \) (Figs. 12E and F), the levels of the \( C_i \) (Figs. 12A and B), and the ratio of \( C_i/C_\ast \) (Figs. 12C and D) are different between the two species. Thus the responses of opening-closing activity of stomata are different for soybean and maize under environmental stresses. With increase of \( A_m \) and WUE, the \( R_{sc} \) of maize increased, and \( R_{sc} \) decreased, both tended to 0.5. In contrast, \( R_{sc} \) and \( R_{sc} \) of soybean remained at about 0.2 and 0.8, respectively (Figs. 10A and B). The CO\(_2\) assimilation of soybean required higher levels of \( C_i \) (Figs. 12A and B) and bigger ratio of \( C_i/C_\ast \) (Figs. 12C and D). Thus, to obtain the same level of \( A_m \) as maize, soybean has to open its stomata more widely to keep small \( r_{sc} \), that is, the stomatal conductance, \( g_{sc} \), usually changed with \( g_e \) to meet the requirement of CO\(_2\) in the physiochemical process of photosynthesis (Fig. 12F). In contrast, as a \( C_i \) plant, maize assimilates CO\(_2\) more efficiently, even in low CO\(_2\) concentration.

Although opening-closing activity of stomata depends on the requirement to CO\(_2\) in physiochemical process of photosynthesis to some degree, the self-regulating function of leaves can minimize the opening of stomata to maximize WUE under environmental stresses. As a result, \( a_1 \) of maize in Eq. (2) was much smaller than that of soybean, that means, \( A_m \) of maize was less sensitive to \( g_{sc} \) than that of soybean (Fig. 4). Therefore, the precision of WUE model of maize was lower than that of soybean (Figs. 7, 8). In this study, an attempt to improve the WUE model as Eq. (5) and Eq. (7) of maize was made using Eq. (20), better result was obtained (Fig. 9), but model with high precision remains to be developed in the future.

**Conclusions**

By the comparison of soybean and maize under water and soil nutrient stresses, it was found that the net assimilation rate, \( A_m \), of maize was a little higher than that of soybean, but the transpiration rate, \( E_m \), of maize was only about one-half as much as that of soybean, as a result, the water use efficiency, WUE, was about two and a half times as much as that of soybean in the same weather conditions. Enhancement of water stresses led to the marked decrease of \( A_m \) and \( E_m \) of the two species, but water stresses of some degree could improve WUE, and this effect is more significant for soybean. As leaf water potential, \( \Psi_L \), became small, \( A_m \), \( E_m \) and WUE all decreased, but the dropping patterns were different from each other: WUE changed with \( \Psi_L \) in a second-order curve relation.
The WUE of two species at high fertilization was higher than that at low fertilization, and this effect was obvious especially for maize.

According to the synthetic model of photosynthesis-transpiration based on stomatal behavior, the WUE models of soybean and maize under water and nutrient stresses were developed. The synthetic model was derived by introducing internal conductance, \( g_{sc} \), for the assimilation and the general equation of the stomatal conductance model, into diffusion models of \( CO_2 \) and \( H_2O \) through the stomata of plant leaves. By means of the WUE models, WUE of soybean and maize under water and soil nutrient stresses were estimated. The WUE values estimated by means of the model agreed well with the measured values for the two species. However, this model tended to underestimate WUE for maize. Although an improvement on the model was made in this study, theoretical consideration still needs further work.

Finally, we made clear that the differences of WUE and the applicability of WUE model between the two species by discussing some physiological factors controlling \( A_m \) and WUE. C3 plants are different from C4 plants in the pathway of photosynthesis, thus the requirement to discuss some physiological factors controlling \( A_m \) as compared with maize, soybean has to open its stomata more widely to keep small \( r_{sc} \). Therefore, the responses of opening-closing activity of stomata to environmental stresses are different for soybean and maize.

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