

Another view of gas exchange model: reflection of leaf surface air to stomatal conductance

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Abstract. A reflection function was established, based on leaf gas exchange process and tested with experimental data of eight kinds of plants, *i.e.* tomato, muskmelon, capsicum, maize, grape, onion, *Haloxylon Ammodendron* Bunge and *Caragana Karshiskii* Kom, with multifarious biological characteristic, water and growing status. The function indicated that the leaf stomatal conductance could be linearly reflected by the ratio of humidity and CO₂ concentration at leaf surface, and the behaviour of its slope could be recognized as an indicator of leaf gas exchange efficiency, which had a negative relationship with leaf water use efficiency (*WUE*). The results maybe increase our understanding of potential influences of leaf stomatal conductance on photosynthetic and transpiration gas exchange and leaf *WUE*.

Introduction

Transport of CO₂ and water vapour (H₂O^v) between plant leaves and atmosphere takes place mostly via stomatal pores because the waxy cuticle covering leaf epidermis is highly impermeable to water and other gases. Stomata have evolved physiological control mechanisms to satisfy the conflicting demands of allowing a net carbon gain while restricting water loss to acceptable levels, under a range of environmental conditions, which are exerted by the environment state feedback; on the other hand the gas exchange processes intensively influence the micrometeorology inside of vegetation canopy (especially the air attached to the leaf surface), *e.g.* temperature and components. This made the components of boundary layer air differ from atmosphere, and the status of leaf surface air may reflect values of stomatal conductance (*gs*) [1,2].

The objective of this study was to evaluate influences of *gs* on boundary layer conditions for photosynthetic and transpiration gas exchange.

Model formulation

Three kinds of gas are involved in stomata gas exchange: carbon dioxide, water vapour (H₂O^v) and oxygen. The relationship of leaf surface air conditions reflecting *gs* can be described as:

$$gs = f(hs, Cs, Os) \quad (1)$$

where *gs* is stomatal conductance; *hs*, *Cs* and *Os* are relative humidity, CO₂ concentration and oxygen concentration at leaf surface, respectively.

Oxygen goes out of stomata pore along with H₂O^v, but its amount is really small compared with atmosphere (0.21 mol/mol). And it has exactly the same behavior and variable quantity just as CO₂, except for opposite direction; they carry same message for the state of *gs*. So we ignored the oxygen concentration, and Eqn. 1 become:

$$gs = k \frac{hs}{Cs} \quad (2)$$

where k is a coefficient. This function indicates that the micrometeorology of leaf surface is influenced by the activity of leaf gs through photosynthesis and transpiration processes, thus it can be identified as ‘reflection’ function for the leaf gs .

Materials and methods

The experiment was conducted at the Shiyanghe Experimental Station for Water-saving in Agriculture and Ecology (37°50'49"N, 102°51'01"E) of China Agriculture University, Gansu Province, China, from 1 April to 10 October 2009. Six kinds of crops, *i.e.* tomato, muskmelon, capsicum, maize, grape, onion, two kinds of perennial desert plants, *i.e.* *Haloxylon Ammodendron* Bunge (*H. Ammodendron*) and *Caragana Karshiskii* Kom (*C. Karshiskii*) were involved in the experiment, with multifarious biological characteristic, water and cultivating status.

Photosynthetically active radiation (PAR), CO_2 and H_2O^v concentrations together with stomatal conductance (gs), transpiration (Tr) and photosynthetic (Pn) rate were measured with an Lci-002/C portable photosynthesis system (ADC BioScientific Ltd., England) in clear days. All the measurements were pursued under various natural weather conditions.

The leaf water use efficiency (WUE) was defined as the ratio of Pn to Tr :

$$WUE = \frac{Pn}{Tr} \quad (3)$$

Apparent quantum yield of photosynthetic CO_2 assimilation (ϕ_c) was calculated as the ratio of Pn to PAR :

$$\phi_c = \frac{Pn}{PAR} \quad (4)$$

Results

Table 1 Gas exchange properties of adult leaves for eight kinds of plants.

	gs [mmol/m ² /s]	Tr [mmol/m ² /s]	Pn [μmol/m ² /s]	WUE [μmol CO_2 /mmol H_2O^v]	ϕ_c [mmol CO_2 /mol photon]
<i>Tomato</i>	500±199	19.36±9.98	31.44±14.95	1.80±0.91	35.82±21.53
<i>Muskmelon</i>	352±157	14.41±9.06	26.86±9.61	2.59±1.13	22.14±10.54
<i>Capsicum</i>	441±236	21.47±10.14	30.60±11.47	1.79±0.83	19.27±11.11
<i>Maize</i>	596±265	18.52±5.01	54.73±23.64	3.04±1.18	28.85±12.20
<i>Grape</i>	53±23	3.25±1.37	8.39±2.77	3.08±1.75	5.30±3.03
<i>Onion</i>	187±134	8.27±4.42	20.72±11.64	2.75±1.37	11.32±7.34
<i>H. Ammodendron</i>	48±35	1.69±1.00	8.84±5.91	5.60±2.61	9.64±8.00
<i>C. Karshiskii</i>	26±11	1.34±0.83	3.89±2.58	3.49±1.92	5.11±4.04

Table 2 Coefficients and estimation precision for leaf stomatal conductance (gs), using Eqn. 2, for eight kinds of plants.

Plants	k	R^2	F	n
<i>Tomato</i>	173.09	0.983	6995**	123
<i>Muskmelon</i>	156.67	0.972	4844**	141
<i>Capsicum</i>	179.48	0.961	1858**	76
<i>Maize</i>	96.39	0.954	680**	34
<i>Grape</i>	99.46	0.944	2088**	124
<i>Onion</i>	98.25	0.975	2881**	74
<i>H. Ammodendron</i>	22.92	0.934	3502**	249
<i>C. Karshiskii</i>	14.73	0.976	10386**	251

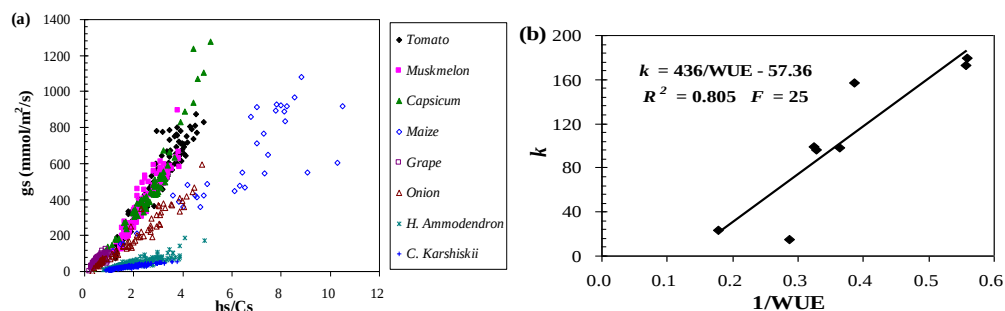


Fig. 1 (a) Scatter diagrams of the leaf stomatal conductance (g_s) and the Eqn. 2 model index (h_s/C_s) for eight species of plants. (b) Relationship between the regressed coefficients (k) of Eqn. 2 and the reciprocal of average water use efficiency ($1/WUE$) for eight species of plants.

There were three species of vegetable, tomato, capsicum and onion, a sprawling fruit, muskmelon, a perennial woody fruit, grape, a C_4 food grain, maize, and two kinds of perennial desert shrubs, *H. Ammodendron* and *C. Karshiskii* involved in the research. Their gas exchange properties (Table 1) were different due to their biological characteristics and weather conditions. For different species the maximum average g_s and P_n was obtained by maize, and it also had extremely big WUE and ϕ_c for its advantageous C_4 photosynthesis pathway. Meanwhile the perennial wood, grape, *H. Ammodendron* and *C. Karshiskii* had smaller average g_s and P_n but largest WUE , as a result they consumed less water and grew slowly. The average g_s , Tr and P_n of annual tomato, muskmelon and capsicum were bigger and had a efficient ϕ_c , but smallest WUE . The largest WUE , tomato, muskmelon, capsicum, maize, Grape, onion, *H. Ammodendron* and *C. Karshiskii* had ever achieved in the measurement, were 6.40, 5.80, 3.45, 5.72, 10.77, 8.34, 15.81 and 15.58 $\mu\text{mol CO}_2/\text{mmol H}_2\text{O}^v$ respectively.

The observed g_s and h_s/C_s values were plotted in Fig. 1 (a), which represented a set of linear relationship, going through the origin of coordinates. Results of the linear regression analysis were listed in Table 2 for each species. The model simulations indicated that Eqn. 2 was able to explain more than 90% of the variations in observed g_s for all tested species. Both the R^2 values and levels of the F -statistic of all the tested species indicated that the estimated regressions significantly ($p < 0.01$) explained the variations in the levels of the various dependent variables, and the biggest R^2 was achieved by tomato. The obtained slopes (k) were variance from 14.73 for *C. Karshiskii* to 179.48 for capsicum; maize, grape and onion had almost the same k values, about 98, and so as to tomato, muskmelon and capsicum, they had another similar k value, about 170.

Discussion

The reflection function (Eqn. 2) linked the leaf surface micrometeorology and g_s via a constant k , which represented a marginal increasing rate, and could be treated as a potential indicator for the relationship between the two factors. Functions with larger k values indicated smaller h_s/C_s when the plants had same g_s , and so implied less leaf gas exchange activities of the plants, since less amount of H_2O^v flowing out of stomata pore (smaller h_s) and less CO_2 diffusing into stomata (larger C_s).

The slopes (k values) of the eight species of plants generally fell into three ranges (Table 2 and Fig. 1 a): 156~179 category for tomato, muskmelon and capsicum; 96~99 category for maize, grape and onion; 14~23 category for *H. Ammodendron* and *C. Karshiskii*. Thus, for this research the relationship between g_s and h_s/C_s appeared to be described by three different slopes: high levels for annual broadleaf herbage, moderate high levels for C_4 gramineous grain (maize), perennial woody

fruit (grape), and perennial liliaceous herbage (onion), and low levels for perennial desert plants. It seemed that the slopes reasonably associated with physiological characteristics of the plant, because they were marked with various gas exchange identities. The effective growth period of annual herbage was so limited that they had to accelerate their metabolism, capturing more solar energy and transporting more water during a short time of comfortable climate. Meanwhile, the desert plant had been developed a more economical system to minimum water loss with considerable assimilation to cope with the extremely dry environment. When k was replaced by Pn , we got Ball-Berry empirical model[3]: $gs=Pn*hs/Cs$. And moreover, there was a significantly linear relationship between k and the reciprocal of average leaf water use efficiency ($1/WUE$, Fig. 1 b).

Conclusions

Leaf gs and the ratio of humidity and CO_2 concentration at leaf surface appeared to be a linear relationship, whose slope could be recognized as a potential indicator of the leaf water use efficiency (WUE). The model slope and WUE showed a negative relationship, and there was a significantly linear relationship between k and $1/WUE$.

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