

光合作用-蒸腾作用-气孔导度的耦合模型及 C₃ 植物叶片对环境因子的生理响应*

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摘要 以叶片的气体传输过程为基础,将蒸腾作用包括在以往光合作用-气孔导度的耦合模型中,建立了光合作用-蒸腾作用-气孔导度的耦合模型。该模型可以模拟边界层导度对生理过程的影响。模拟了 C₃ 植物叶片对环境因子,如光照、温度、湿度、边界层导度和 CO₂ 浓度等的生理响应(光合作用、蒸腾作用、气孔导度)以及 C_i 和水分利用效率的变化。在环境因子变化于较大范围的情况下,模拟结果符合许多实验结论。

关键词 光合作用,蒸腾作用,气孔导度,边界层导度,耦合模型

SIMULATION OF THE PHYSIOLOGICAL RESPONSES OF C₃ PLANT LEAVES TO ENVIRONMENTAL FACTORS BY A MODEL WHICH COMBINES STOMATAL CONDUCTANCE, PHOTOSYNTHESIS AND TRANSPIRATION*

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Abstract Transpiration element is included in the integrated stomatal conductance-photosynthesis model by considering gaseous transfer processes, so the present model is capable to simulate the influence of boundary layer conductance. Leuning in his revised Ball's model replaced relative humidity with VPD_s (the vapor pressure deficit from stomatal pore to leaf surface) and thereby made the relation with transpiration more straightforward, and made it possible for the regulation of transpiration and the influence of boundary layer conductance to be integrated into the combined model. If the differences in water vapor and CO₂ concentration between leaf and ambient air are considered, VPD_s , the evaporative demand, is influenced by stomatal and boundary layer conductance. The physiological responses of photosynthesis, transpiration, and stomatal function, and the changes of intercellular CO₂ and water use efficiency to environmental factors, such as wind speed, photon flux density, leaf temperature and ambient CO₂, are analyzed. It is shown that if the boundary layer conductance drops to a level comparable with stomatal conductance, the results of simulation by the

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model presented here differ significantly from those by the previous model, and, in some cases, are more realistic than the latter.

Key words Photosynthesis, Transpiration, Stomatal conductance, Boundary layer conductance, Integrated model

Physiological responses to the changing environment have been intensively studied in the past decade on all levels, from leaf, canopy, region up to the global one. Simulation models of physiological processes in response to environmental factors is the basis of the study of the interactions between plant and environment, such as the effects of global warming and elevated atmospheric CO_2 on vegetation, and the role in plant cover in determining climate change. Leaf level is the basic level in the study of interactions between vegetation and atmosphere at which physiological regulation by feedback processes of the environmental factors as the inputs of the model are not involved. The model at the leaf level can also be used in the modeling of processes on larger scales by scaling up^[1,2].

The stoma is a well evolved organ which responds to environmental factors in such a manner that it not only protects the plant from excessive water loss, but also maximize water use efficiency^[3]. Its regulation is a key element in mass flow through the soil-plant-atmosphere continuum (SPAC) with respect to water loss and carbon gain.

Though much is known about stomatal behavior, some mechanisms have not yet to be clarified. The mathematical simulation models on stomatal conductance are mostly at a semi-empirical level, except that Upadhyaya *et al*^[4], and Fu & Wang^[5] tried to construct mechanistic models which include water potential, photosynthetic electron transport rate and ion fluxes into or out of the guard cells. These models, though analytical, are useful in theoretical pursuits only since it contains some variables which are not readily measurable, and therefore can not be used on data taken by ordinary instruments, which limits their application.

A semi-empirical model proposed by Ball *et al*^[6] summarized the linear relation between stomatal conductance and an index relating the assimilation rate of the leaf, and relative humidity and CO_2 concentration over the leaf surface. The stomatal model can be combined with photosynthesis model and vegetation evapotranspiration model, and is widely used in the analysis of many kinds of physiological-ecological problems on different scales, for example, in modeling evapotranspiration of a plant canopy^[7].

In Ball's equation, stomatal conductance and photosynthesis are interdependent, and a photosynthesis submodel is needed in the solution. So Leuning^[8] proposed to solve a combined photosynthesis-stomatal conductance model. By combining Ball's model with Farquhar's intercellular biochemical model of photosynthesis, Collatz *et al*^[9,10] proposed that boundary layer conductance (g_b) over a leaf surface may be an important factor causing midday depression, both too large or too small a value of g_b will cause a decrease in photosynthesis. But the relation between stomatal conductance and stomatal conductance index ($An_h s / C_s$) will change when g_b changes, because it is through the response to C_s (leaf surface CO_2 concentration) that stomata response to C_a , under conditions where g_b is small, there is a substantial difference between C_s and C_a ^[11] (ambient CO_2 concentration). Reynolds *et al*^[12] used an integrated model to predict the effects of elevated CO_2 on photosynthesis. Shi and Wang^[13] used a combined model to simulate WUE (water use efficiency) as influenced by environmental factors, such as CO_2 concentration, light intensity, and VPD . A number of studies suggested that stomata respond to VPD (vapor pressure deficit) in a better defined way than to relative humidity (h_s), so Leuning^[14] revised Ball's model using VPD as the evaporative demand parameter driving transpiration instead of h_s . The effects of the boundary layer conductance have been

studied by Aphalo and Jarvis^[15], and a mathematical relation between VPD and g_b and g_s (stomatal conductance) was deduced by using gaseous diffusion equation.

Although there are many studies on simulation of stomatal function and combined models, systematic analysis of physiological responses to environment has rarely been done. It is of primary importance in model building to construct a sound framework so that observed phenomena can be simulated under widely different circumstances. Numerical analysis of physiological responses is important to study the sensitivity to input factors of the model itself, and provide information for researchers to improve this kind of models. Models of physiological responses to environmental factors have a wide range of use in the modeling of crop yield formation, and can be expanded to models of plant-atmosphere interaction by scaling up.

The objectives of this study are (1) to incorporate transpiration into the model in which C_s and VPD_s will not be given directly as inputs but as variables controlled by mass diffusion fluxes and the concentration gradients, which is influenced by changes of boundary layer conductance; (2) to evaluate the effects of environmental factors, such as wind speed, vapor pressure deficit, irradiance, temperature and ambient CO_2 concentration on the processes of assimilation, transpiration, stomatal function and the changes in the intercellular CO_2 (C_i) and WUE ; and (3) to reveal the relation between photosynthesis, transpiration and stomatal conductance under changing environmental factors.

1 The MODEL

The model combines the photosynthesis-stomatal conductance submodel proposed by Leuning^[14] and the integrated submodel of transpiration proposed by Aphalo and Jarvis^[15].

1.1 Stomatal Conductance Submodel

Steady-state models of stomatal function, which are more popular than dynamic ones, may be classified into three types^[16]: multiple correlation models, phenomenological models and models based on hypothetical mechanisms of stomatal regulation. The multiple correlation models, expressing stomatal conductance as linear multiregression function of light, temperature, humidity and water potential, is of little use in analyzing mechanisms involved. In phenomenological models, a representative one of which was proposed by Jarvis^[17], has been widely adopted by modellers. The model may fit well to experimental data of stomatal conductance in response to single environmental factor when other factors are kept constant.

$$g_{sc} = f_1(Q) f_2(T_{leaf}) f_3(VPD_a) f_4(C_a) f_5(\psi) \quad (1a)$$

where g_{sc} , the stomatal conductance to CO_2 , is expressed as the function of irradiance (Q), leaf temperature (T_{leaf}), water vapor pressure deficit from leaf to atmosphere (VPD_a), CO_2 concentration (C_a) and leaf water potential (ψ).

Wong *et al.*^[18] found that the regulation of stomata is to hold C_i constant. In a steady state condition, there is a linear relation between g_{sc} and An when C_s and hs are not changing^[19]. On this basis, Ball's stomatal model is presented as follow.

$$g_{sc} = m \frac{Anhs}{C_s} + b \quad (1b)$$

where An is net photosynthetic rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$); hs and C_s are relative humidity and CO_2 concentration over leaf surface respectively; m and b are parameters, the latter being the intercept on the coordinate g_{sc} near zero. $Anhs/C_s$ is referred to as stomatal conductance index. Since Eq. 1b is not applicable to low CO_2 concentrations, Leuning^[8] used $C_s - \Gamma$, instead of C_s , where Γ is the CO_2 compensation concentration, to give a better fit. Recent experiments revealed that stomata respond to evaporative demand (VPD) more than to relative humidity of air^[20,21]. By adopting these modifications, Leuning^[14] proposed a revised form of Ball's model, viz.,

$$g_{sc} = m \frac{An}{(C_s - C_i)(1 + VPD_s/VPD_0)} + g_{s0} \quad (1c)$$

where g_{s0} , the intercept, is equivalent to b in Eq. (1b); VPD_0 is a parameter.

1.2 Photosynthesis submodel

Farquhar^[22] has generalized the main aspects of intercellular bioprocesses with a biochemical model. One of the input factors needed is intercellular CO₂ concentration, which depends on the rate of photosynthesis and gaseous diffusion conductance controlled by stomata. The stomatal conductance and photosynthesis submodels are interdependent, so a combination of them is needed to predict physiological responses to environmental factors. The model used here was proposed by Farquhar *et al.*^[22] and von Caemmerer & Farquhar^[23]. The equations and parameters used here are from Leuning^[14]. So the assimilation rate may be described as

$$An = \min\{Ac, Aq\} - Rd \quad (2)$$

where Ac and Aq are the rates of photosynthesis limited by Rubisco activity and the rate of RuP₂ regeneration through electron transport, respectively. Daytime respiration (Rd) depends mainly on leaf temperature. The term $\min\{Ac, Aq\}$ represents the minimum of the two values within the brackets, of which Ac depends on C_i and temperature and Aq depends not only on C_i and temperature, but also on irradiance.

1.3 Transpiration Submodel

Stomata are sensitive to both CO₂ and water vapor concentration with their aperture enlarging as CO₂ concentration or VPD decreases. In previous combined model, VPD_s is taken as an environmental factor. When boundary layer conductance is high enough to be nonlimiting, a situation always satisfied in the leaf chamber, the relation described in the Ball's stomatal conductance model holds. But under natural conditions, the influence of changes in boundary layer conductance, which depends mainly on wind speed, always need to be taken into account. When g_b is low, the humidity difference between ambient air and leaf surface may not be negligible, and a similar situation also exists with CO₂ concentration. Taking this into consideration, Aphalo and Jarvis^[15] derived an expression of VPD_s , the VPD between intercellular space and the air layer just above the leaf surface, as a function of VPD_a (the VPD between intercellular space and ambient air), g_{sw} and g_{bw} as follows under the assumption that $T_{leaf} = T_a$,

$$VPD_s = VPD_a(1 - g_{nw}/g_{bw}) \quad (3)$$

where VPD_a is water vapor pressure deficit from intercellular and ambient air (Pa); g_{nw} and g_{bw} are total conductance and boundary layer conductance to water vapor ($\text{mol m}^{-2} \text{s}^{-1}$), respectively. In fact, Eq. 3 is derived from the equation for transpiration, in which VPD_s represents the driving force for transpiration.

This relation is derived from mass flux equation for steady state. We have also

$$E = g_{sw}VPD_s \quad (4)$$

where E is transpiration rate, g_{sw} is stomatal conductance to water vapor.

The relation between g_{sw} with g_{sc} and overall stomatal conductance to CO₂ (g_{tc}) can be expressed in terms of g_{sc} and g_{bw} as follows.

$$g_{sw} = 1.6 g_{sc} \quad (5)$$

$$g_{tc} = (1/g_{sc} + 1.37/g_{bw})^{-1} \quad (6)$$

$$g_{bw} = (1/g_{sw} + 1/g_{bw})^{-1} \quad (7)$$

in steady state, by using diffusion equation, the following relations hold:

$$C_s = C_a - An/g_{bc} \quad (8)$$

$$C_i = C_a - An/g_{tc} \quad (9)$$

where g_{bc} is boundary layer conductance to CO₂, the saturated vapor pressure at any leaf

temperature is calculated by the Goff-Gratch equation.

1.4 Model Solution

Nine equations (1c) ~ (9), (including A1 ~ A7 used by Leuning^[14]), are used to describe the relation between nine unknown variables and consist of a set of complete nonlinear equations which can be solved by iteration. A numerical approach similar to that of Collatz *et al*^[19] can be used to couple the submodels. In finding the solution, the value of C_i is given first, and substituted into the biochemical photosynthesis model (Eq. 2) and to get A_n . Then stomatal conductance is calculated from the stomatal model (Eq. 1c), and a new C_i is found by the diffusion model (Eq. 9). These steps are repeated until the change in C_i is less than a certain small value of allowance. All of the physiological variables are solved simultaneously. The negative physical and physiological feedback processes in the model guarantee the convergence of the set of equations used in respective of the kind of changes of environmental factors.

Parameters in the photosynthesis submodel are taken from Leuning^[14], with $J_{max0} = 50$ and $V_{cmax0} = 25 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Respiration (R_d) in Eq. 2 is 1% of V_{cmax} , the maximum catalytic activity of Rubisco in the presence of saturating levels of RuP₂ and CO₂. In the stomatal conductance model, $VPD_0 = 1500 \text{ Pa}$, $m = 20$.

2 RESULTS

2.1 Boundary layer conductance

In Fig. 1, it is demonstrated that when g_{bc} is initially small, its rise due to decrease in boundary layer thickness caused by wind will induce a sharp increase in total conductance, and thereby in C_i , assimilation and transpiration rates. Since stomata respond to CO₂ concentration, an increase in g_{bc} may elevate C_s and enlarge VPD_s , both of which have the effect of decreasing g_{sc} , and, therefore, diminish the extent of increase in A_n caused by wind, but not totally abolish the increase. As there is an additional mesophyll resistance for photosynthesis, the diminishment of g_{bc} will have a lesser effect on A_n than on E . So the water use efficiency (WUE) will increase with decreasing g_{bc} . It means that the lowering of g_{bc} has a more severe effect on water loss than on photosynthesis. Some model experiments also suggest that in warm environments with low radiation, large leaves with thick boundary layers would have an advantage in WUE through reduced transpiration.

When g_{bc} reaches a value of about $0.5 \text{ mol m}^{-2} \text{ s}^{-1}$, the response of physiological factors will no longer change with any increase of it. It means that the extents to which surface water vapor and CO₂ concentration departs from that in the ambient air is very small, the effect of g_{bc} could be neglected when g_{bc} is much greater than g_{sc} . But in a similar stomatal conductance-photosynthesis model^[9], the result of simulation is that photosynthesis is inhibited under both high and low boundary layer conductance, and is high when g_{bc} takes a medium value. They included midday depression of transpiration due to stomatal closure as a result of positive feedback mediated by the boundary layer conductance, for high or low values of g_{bc} which will lead to excessive drying or heating, respectively, of the air at the leaf surface^[24]. Such simulations show that the dependence of leaf transpiration on boundary layer conductance is such that maximum transpiration and photosynthesis occur at intermediate values of g_{bc} . But we argue that the effect of g_{bc} may not be of great importance when it exceeds a certain value, so that differences of CO₂ concentration and water vapor between leaf and ambient air are very small. The earlier model includes leaf energy balance submodel, which made the response quite complex. If we consider only the effect of g_{bc} under laboratory conditions, at a certain leaf temperature, the excessive drying does not exist. Because, pushing to the limit, even when g_{bc} is infinite, the e_s can only be as low as e_a , and not lower.

Fu and Wang^[5] found in their experiment that the relationship between stomatal conductance

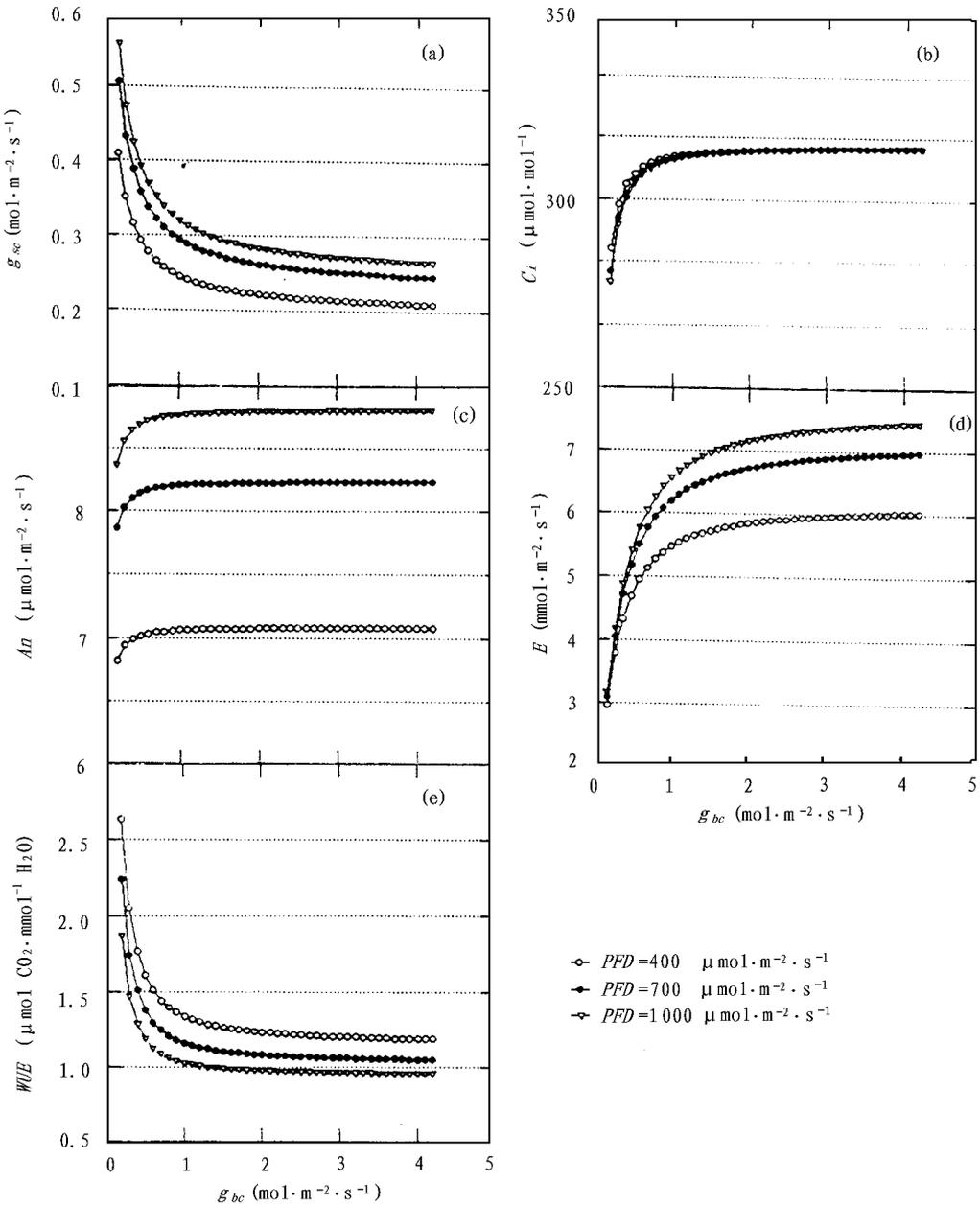


Fig. 1 Simulated physiological responses to boundary layer conductance at different irradiances e_a , 1200 Pa; C_a , 350 $\mu\text{mol}\cdot\text{mol}^{-1}$; T_{leaf} , 25 °C; PFD , 400, 700, 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; An , net assimilation; E , Transpiration; g_{sc} , Stomatal conductance to CO₂; g_{bc} , Boundary layer conductance to CO₂; C_i , intercellular CO₂; WUE , Water use efficiency.

and stomatal conductance index (An/g_s) will change with g_{bc} . The earlier model did not include the influence of changes in g_{bc} on C_s and VPD_s , which makes some of the simulation results relating to g_{bc} questionable. The present model can simulate these influences (Fig. 2).

2.2 VPD_a

In the simulation, VPD_a is varied by changing the value of ambient water vapor pressure (e_a).

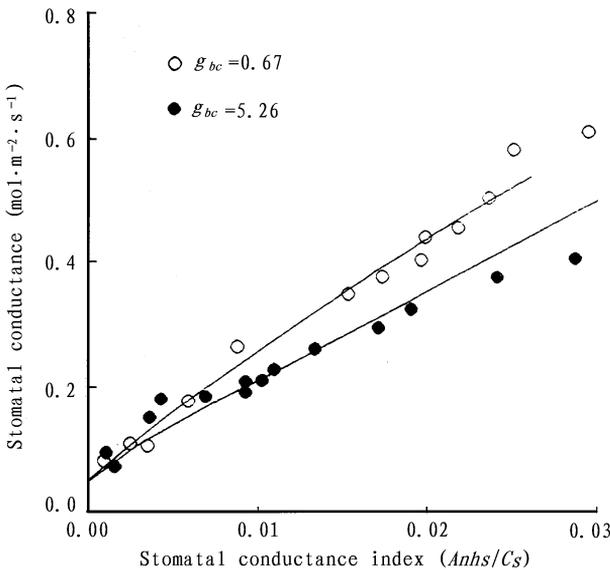


Fig. 2 Simulation of and observation on the influence on boundary layer conductance on the relation between stomatal conductance and stomatal conductance index ($Anhs/C_s$)

The reference conditions for the simulation were $T_{leaf} = 25$, $C_a = 350$ $\mu\text{mol mol}^{-1}$, $e_a = 1000$ Pa, and $PPFD$ varied from 70 to 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Parameters of the model were $m = 20$, $VPD_0 = 1000$ Pa, $g_{s0} = 0.05$. Data are from Fu and Wang^[5].

decreases with increasing VPD_a , this relation is also shown in the experiment of Comstock^[25].

VPD_a is the force driving water vapor from leaves to the atmosphere, transpiration is affected also by the conductance of stomata, which in turn responds to the VPD_a in their micro-environment, and thus forming a feedback loop. This is the feedback effect of stomata's response to humidity deficit, i. e., an increase in the rate of transpiration will cause a decrease in stomatal conductance, which in turn will decrease the rate of transpiration by some extent. So transpiration increases with an increase in VPD_a , but to a lesser degree. Feedforward occurs when the imposed change in the environmental factors affecting transpiration rate causes a change in conductance independent of the resulting change in the transpiration rate. Although many other species do not exhibit feedforward reaction, cases in which transpiration rate declined with increasing evaporative demand have been found by many researchers as listed by Farquhar^[28]. From Fig. 3d, E always increases with increasing VPD_a , so obviously, this model cannot simulate the feedforward response of stomata to humidity deficit.

When VPD_a changes, workers are always concerned with the interrelation between the physiological responses. A nearly linear decrease of conductance with increasing transpiration rate is presented in stomatal response to humidity (Fig. 4). Monteith^[29] selected fifty-two sets of measurements appearing in seven publications, and showed that of the 271 individual measurements of stomatal conductance, 234 showed a strong evidence to support this relation.

2.3 Leaf temperature

Temperature affects photosynthesis and stomatal conductance in two ways, one is on the intrinsic speed of biochemical processes of photosynthesis, the other is on VPD_a through its effect on

In Fig. 3, it can be seen that g_{sc} declines hyperbolically with an increase in VPD_a as observed in many studies. The response of stomata to a change in VPD_a is closely related with the process of transpiration. C_i declines almost linearly with an increase in VPD_a , because of stomatal closure, and An declines with increasing VPD_a by a weak accelerating rate which is caused by a C_i value which is progressively more limiting to photosynthesis. Comstock^[25] has found this relation to hold in his experimental study. The results of simulation imply that C_i responds to VPD_a more evidently than to other stimuli. Since small changes in humidity can affect stomata without directly affecting assimilation rate in many species^[26], C_i varies with humidity^[27]. It is pointed out that there is a nearly linear relation between C_i and VPD_a in Leuning's revised model which is shown in Fig. 3(b). WUE decreases with increasing VPD_a more rapidly than any other elements, as transpiration increases and photosynthesis

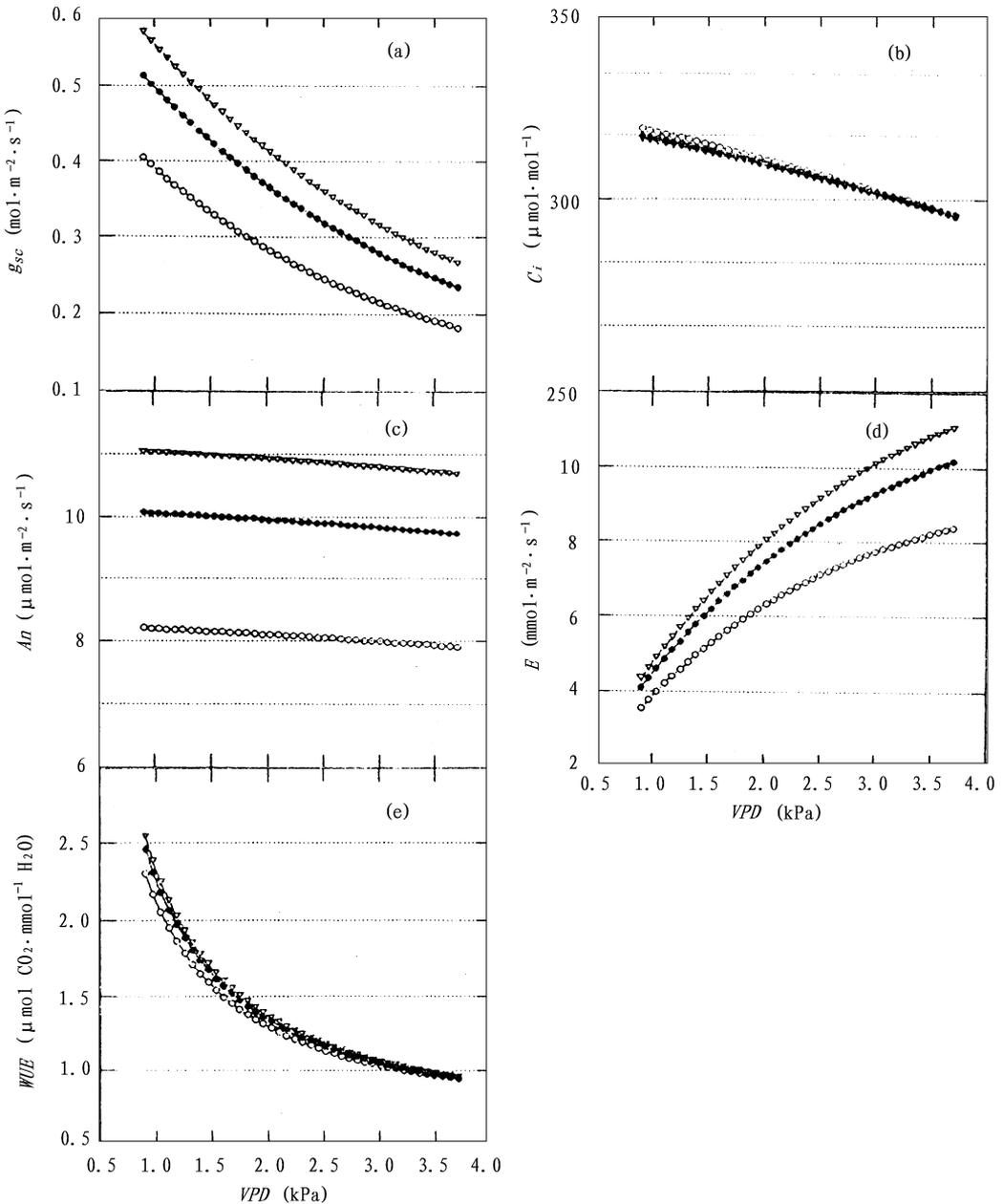


Fig. 3 Simulated physiological responses to vapor pressure deficit at different irradiances. The conditions are the same as in Fig. 1, except for boundary layer conductance, which is 1.0 mol CO₂ m⁻² s⁻¹.

the saturated intercellular vapor pressure. According to the chain of effects discussed in the preceding paragraphs, photosynthesis decreases with increasing VPD_a because of the limitation caused by stomatal closure.

Fig. 5 shows that assimilation, transpiration and stomatal conductance vary with temperature as one-peaked curves. Measurements of stomatal conductance response to temperature gave the optimum-type responses^[30] like many other biological responses. The optimum temperature of

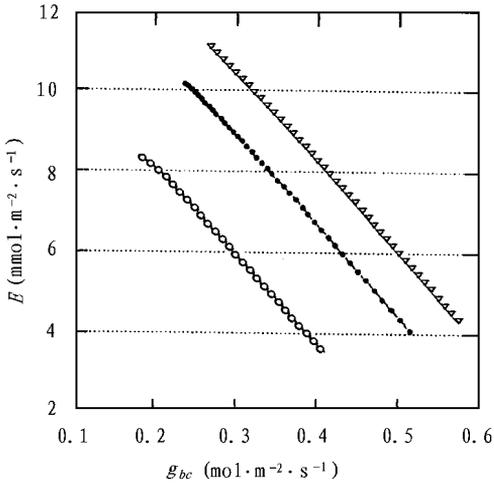


Fig. 4 Transpiration rate versus stomatal conductance under varying VPD . Data are the same as in Fig. 3.

stomatal conductance is lower than that of assimilation. Although stomatal conductance is proportional to assimilation in experimental studies under certain conditions^[31~33], an increase in temperature will cause an exponential increase in VPD_a which will make stomatal conductance decline hyperbolically. So the magnitude of decline in g_{sc} is greater than those in A_n and E . When leaf temperature is lower than the optimum temperature for stomatal conductance, E increases sharply with increasing T_{leaf} . Both VPD_s and g_{sw} , the two factors determining transpiration rate, increase with increasing temperature. When leaf temperature exceeds slightly its optimum value for stomatal conductance, transpiration will continue to increase before the decrease of g_{sw} is stronger than the increase of VPD_s . When T_{leaf} rises further, a point will eventually be reached when the stomata close so tightly that transpiration decreases despite of the very

large VPD_s . WUE declines monotonously with an increase in temperature, because the increase in VPD_a is much steeper than that in CO_2 concentration deficit. From the analysis made above it follows that C_i/C_s is determined mainly by the changes in g_{sc} caused by changes in VPD_a , so an increase in temperature causes a monotonous decrease in C_i .

2.4 Irradiance

Irradiance affects physiological processes in two ways: (1) physiologically providing the energy for photosynthesis, and (2) physically affecting the leaf energy balance, which determines leaf temperature. The former part also includes direct and indirect responses of stomatal conductance, e. g., pigments within the guard cells absorb the light and then the guard cells respond to CO_2 ^[34]. Under natural conditions, both parts should be taken into consideration. Here we only take account of the former, omitting the leaf energy budget, and the leaf temperature is assumed constant so as to compare with some experimental results under laboratory conditions, and to observe the two effects separately.

The curves are the results of simulation for different leaf temperatures. The receptor for light is the photosynthetic system, which is inside the mesophyll. So firstly, A_n increases with PF along the Michaelis-Menten curve. The intersection of curves in Fig. 6a shows the influence of temperature on both photosynthesis and respiration. Secondly, C_i decreases with increasing PF , so as to enlarge the difference between C_a and C_i , but the change is not great over a wide range of PF and is evident when irradiance is weak (Fig. 6b). This phenomenon always exists as first proposed by Scarth (1932) that an increase in irradiance can cause an increase in photosynthesis, leading to a decrease in C_i , and then stomata open in response to the decrease in the C_i ^[34]. Wong^[31] found that A_n and g_{sc} change in the same proportion, so that C_i changes very little over a wide range of PF . In most of the species examined, when light intensity increases, photosynthesis and conductance increase, but C_i decreases obviously at low PF , and comes to a fairly constant value when light intensities are above 10 percent of full sunlight^[35].

When VPD_a is kept constant transpiration is determined mainly by g_{sc} . Both photosynthesis and transpiration are increasing with irradiance. Although their ratio, WUE , increases with

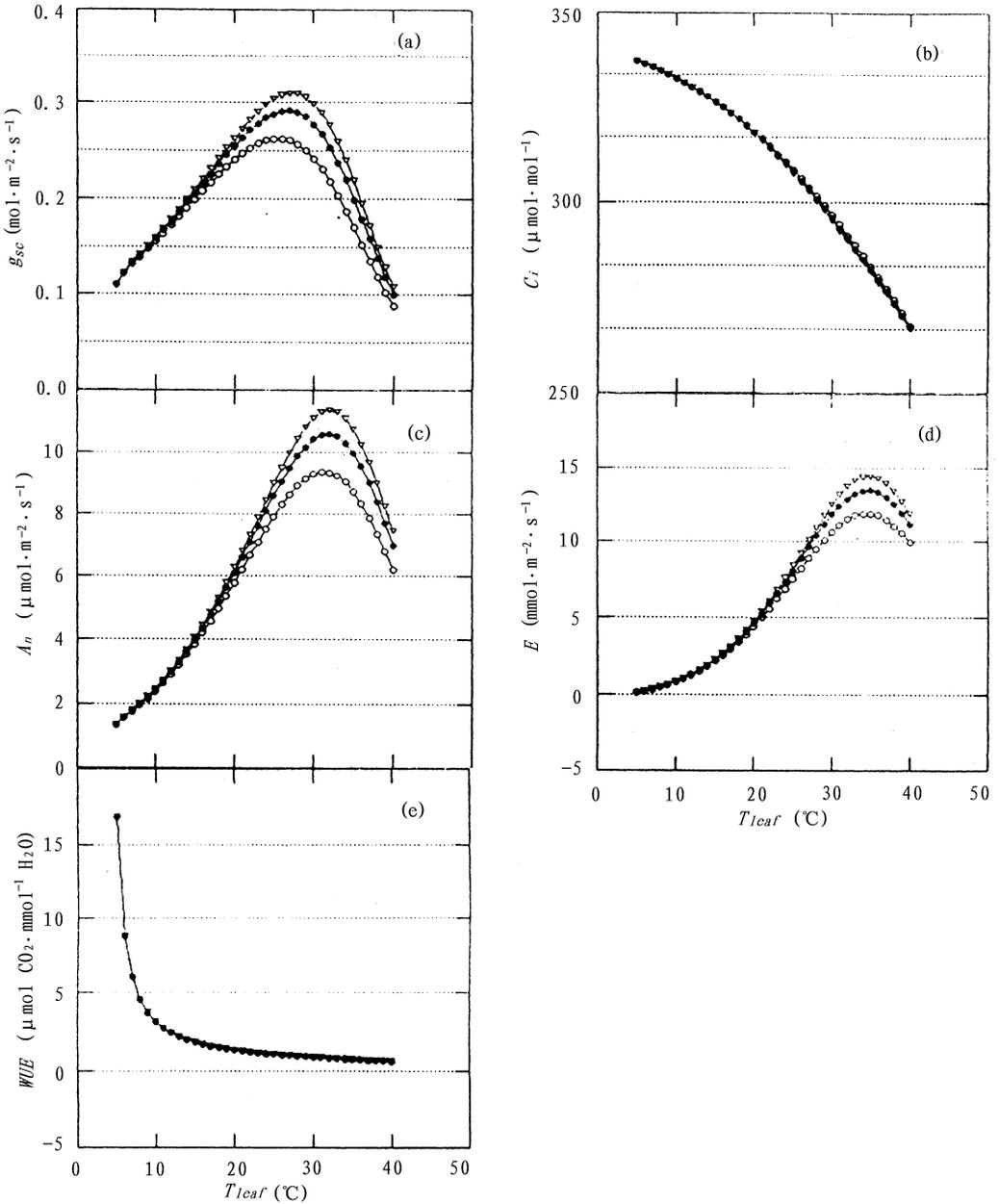


Fig. 5 Simulated physiological responses to leaf temperature at different irradiances
The conditions are the same as in Fig. 1, except for boundary layer conductance, which is 1.0 mol CO₂ m⁻² s⁻¹.

irradiance (Fig. 6e), its increase rate is smaller than that of either A_n or E . This means that an increase in irradiance increases photosynthesis more than transpiration, by contrast with the effect of an increase in boundary layer conductance which is greater on transpiration than on photosynthesis (Fig. 1e). When PFD exceeds about 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the increase of the WUE is not significant, as Shi and Wang^[13] found in their experiment.

For relation between physiological factors, it is shown that g_{sc} increases as A_n increases.

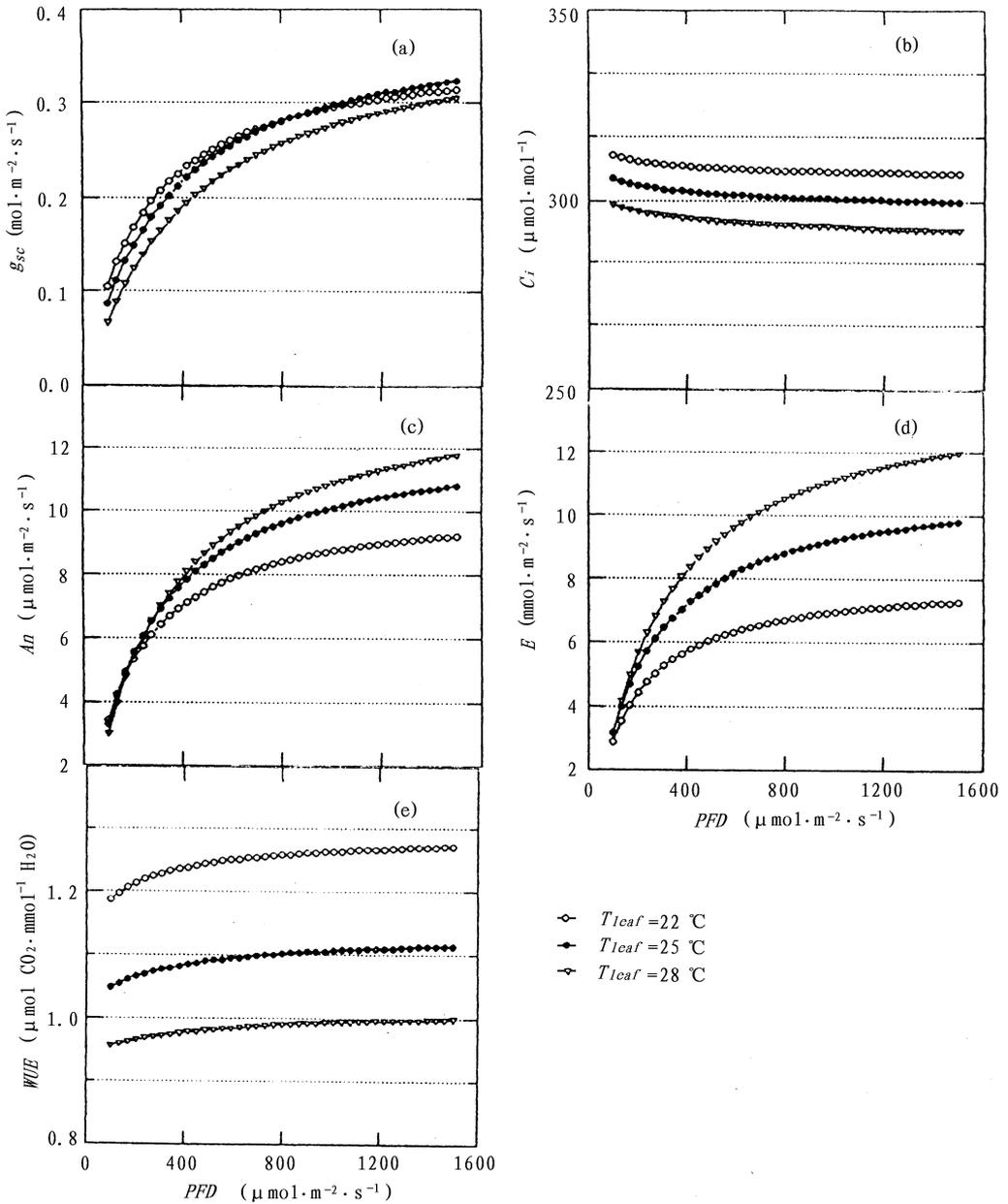


Fig. 6 Simulated physiological responses to PFD at different leaf temperatures

The conditions are the same as in Fig. 1, except for the boundary layer conductance, which is $1.0 \text{ ml CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

When g_{sc} increases, VPD_s decreases from Eq. 3, which diminishes somewhat the degree of increase in transpiration rate with increasing g_{sc} (Fig. 7).

2.5 Ambient CO₂

Physiological response of plant to elevated CO₂ concentration can be divided into two kinds. The short-term one does not include the change in photosynthetic system, whereas a long-term one includes the acclimation of photosynthetic activity to elevated CO₂ [36]. Here a short term response in

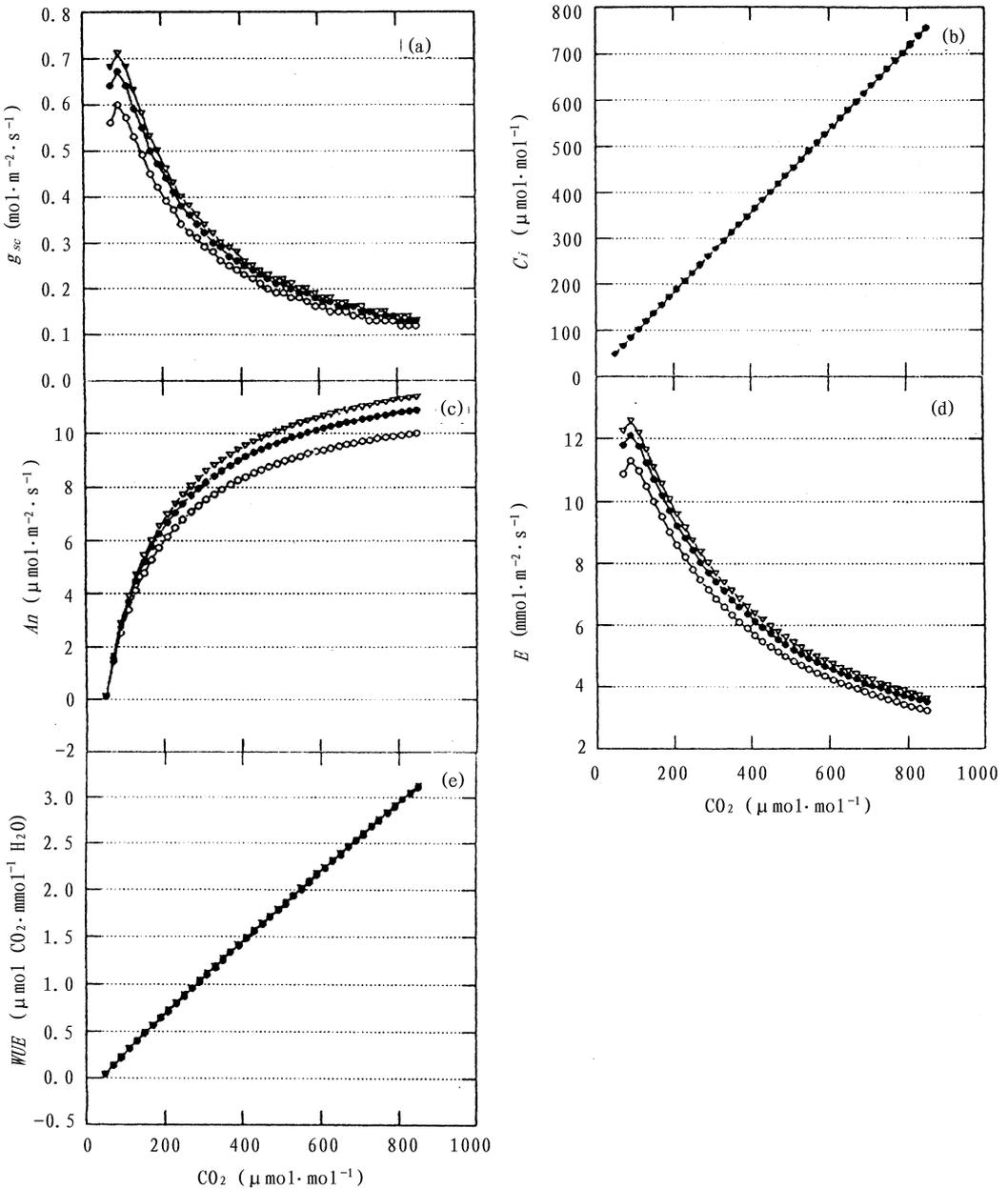


Fig. 7 Simulated physiological responses to ambient CO₂ concentration at different irradiances
 The conditions are the same as in Fig. 1, except for the boundary layer conductance, which is 1.0 mol CO₂ m⁻² s⁻¹.

a steady state is considered.

In Fig. 7, a nearly linear increase in C_i with an increase in ambient CO₂ is generated by the model. It shows that the intercept is near zero, so C_i/C_a , or more precisely C_i/C_s is almost constant, as was found by many workers, e. g. Wong^[18,31]; Sharkey and Raschke^[37]; Morison and Jarvis^[35] among others.

Because there is a linear relation between C_a and C_i (Fig. 7b), the relation between An and

C_a , shown in Fig. 7c can also be taken as the relation between An and C_i . The relation between An and C_a obeys the Michaelis-Menten equation. As An increases and stomatal conductance decreases with an increase in C_i , a stomatal sensing of C_i occurs. In many experiments, the response of stomatal conductance to CO_2 concentration is generally curvilinear, showing larger changes in response to concentrations increase below $300 \mu\text{mol} \cdot \text{mol}^{-1}$ than under higher concentrations. Eq. 1b should not be used when $An = 0$ (when $PFD < 50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or $C_s < 100 \mu\text{mol} \cdot \text{mol}^{-1}$), and when the use of $C_s -$ instead of C_s in Ball's model will fit well at low CO_2 concentrations^[81]. In some reports, maximum conductance occurred at an ambient CO_2 of $100 \mu\text{mol} \cdot \text{mol}^{-1}$ ^[38,39]; in most of others, at $0 \mu\text{mol} \cdot \text{mol}^{-1}$. We have found that the nature of stomatal conductance at low CO_2 may correlate closely with CO_2 compensation point in the simulation. The peak of g_{sc} at high is obvious, and occurs at higher CO_2 concentrations than at small.

Transpiration also declines with an increase in CO_2 concentration, in the same pattern as stomatal conductance when VPD_s is nearly constant, and so WUE increases with increasing CO_2 nearly linearly. The extent to which WUE increases is about 100 percent under doubled CO_2 concentration, as is shown in Fig. 7e. Morrison and Gifford^[40] found that under doubled CO_2 concentration, a 67% increase in WUE on average was observed for young plants. Many experiments found photosynthesis and WUE increases with increasing CO_2 concentration^[13, 39-45].

3 DISCUSSION

(1) The integrated model presented here is capable of simulating physiological responses to boundary layer conductance, whereas the previous models can not. The difference of the model from previous one is the consideration of gaseous transfer into and out of stomata. Ball's model is based on the results that g_{sc} varies in proportion to An when C_s and h_s are held constant, which is found by Wong^[18]. It has the same meaning as to say that C_i/C_s is constant on the condition that humidity is not changing. In this kind of model, C_i is determined by C_s and VPD_s , and therefore if C_s and VPD_s are given input factors, C_i could be obtained directly. So in the biochemical model of photosynthesis, An can be determined when T_{leaf} , PFD and C_i are known, g_{sc} can be calculated by the stomatal model.

In the present model, after g_b is incorporated into the combined model, C_s and e_s are no longer taken as constant, and are therefore not inputted into the model as constants, but are variables in the combined model. It means that C_s and VPD_s are taken as variables controlled by physiological and ecological factors. For example, when irradiance changes, the change in g_{sc} will induce changes in C_s and e_s . So C_i is not solely dependent on VPD_s as inferred from the previous model in Eq. 11, but changes also with irradiance. Also assuming that C_i/C_s is proportional to VPD_s by taking g_b into account, and VPD_s will change with other environmental factors, such as PFD . C_i also varies with PFD which is a regular phenomenon in experiment, when other factors are kept constant. So more realistic results will be obtained.

In this study, a comprehensive numerical analysis of the model is done. Most of the results of simulations fit reasonably well with experimental results. Such as the fact WUE increases linearly with ambient CO_2 (Fig. 6e), the relation between transpiration and stomatal conductance under varying atmospheric humidity shows a response of stomata to leaf water loss (Fig. 4).

Stomatal response to increasing CO_2 usually take the shape of either a one-peaked or persistent-declining curve. Simulations show the location of peaks of response lines of stomatal conductance to CO_2 as determined by the compensation points of photosynthesis. This result needs experimental verification.

There are still some problems in the model. For example, under different CO_2 concentrations

and $PF D$'s, photosynthesis has saturated points for light and CO_2 , when CO_2 concentration or $PF D$ exceeds the points, photosynthesis will not increase with the factors, but in the photosynthesis model, even under high $PF D$ or CO_2 concentration the photosynthesis rate still increase slightly. Whether the WUE inferred from the simulation of photosynthesis and transpiration gives a reasonable results should be tested by experiment.

(2) Under water stress condition, there are still many problems which need be studied, such as the relation between C_i/C_s and VPD_s , and the effect of water stress on stomatal conductance through electron transport of photosynthesis or the guard cell water potential.

(3) In elucidating the mechanisms of stomatal response, it is advisable to construct a dynamic model with experiments on a time scale of minutes. The time courses of changes in An , C_i and g_{sc} are different under different levels of CO_2 concentration, $PF D$ and VPD_a , because each driving variable may be sensed by a particular receptor in the plant, and the other physiological processes will react as feedbacks. A change in each environmental variable will cause a chain of physiological events, the final steady state is determined by the sequence of events, or, to put in other words, the system has a history, that will make the system very complicated.

4 CONCLUSIONS

The system of models developed here generalizes the physical and eco-physiological processes and interactions or regulation mechanisms at the leaf level. The sensitivity of the model was examined in a wide range of each environmental factor, i. e., boundary layer conductance, water vapor deficit, ambient CO_2 concentration, temperature, and irradiance. Numerical simulations give predicted values of physiological responses similar to those observed in many experimental studies, and sometimes more realistic than those inferred from previous models. Since boundary layer conductance and leaf temperature are closely related to wind speed or air temperature and irradiance, respectively, the combined model can be easily applied to natural conditions after the physiological parameters in the model for given plant types are determined in experiment, in which the inputs of the model are atmospheric variables, such as wind speed, humidity, temperature, solar radiation and atmospheric CO_2 concentration. A leaf energy balance model can be included in the leaf temperature model and a photoinhibition submodel should be considered in the studies on diurnal variations in the nature of physiological processes on fine days. The integrated model can be scaled up from a leaf to the canopy and expanded to the simulation of the interactions between vegetation and environment.

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