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Simulation of leaf photosynthesis of winter wheat on Tibetan Plateau and in North China Plain

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Abstract

Photosynthetic rate of winter wheat was measured in 1995 and 1996 at Lhasa (29°41'N, 91°20'E, 3688 m a.s.l.) on the Tibetan Plateau under the extreme conditions of the highest solar radiation and lowest CO₂ partial pressure on earth. Similar measurements were also made in the North China Plain (Yucheng, 36°57'N, 116°36'E, 28 m a.s.l.) in 1998. It has been shown that photosynthesis was greatly inhibited by high light intensities on the plateau. As diurnal changes in temperature was great, temperature also played an evident role in causing diurnal variation of photosynthesis on the plateau.

A mathematical description of decline of maximum photosynthesis with light intensities due to photoinhibition or photooxidation in plant was developed. The relation is integrated into a leaf photosynthesis model, which includes the rate-limiting biochemical processes of photosynthesis and physiological processes of stomatal regulation. Photosynthesis of wheat under field conditions on Tibetan Plateau was simulated. The model was also verified with the observation of photosynthesis of winter wheat leaves in the North China Plain. The result shows that the model can simulate photosynthetic rate of crops in field fairly well. This model provides a method to calculate plant productivity, especially for plants under plateau climate with high solar radiation and it is also applicable to plant grown in places at low altitudes. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Photosynthesis; Solar radiation; Temperature; Model; Wheat; Tibet

1. Introduction

Tibetan Plateau is the highest plateau on earth, which covers 1.2 million km² of area with an

average height of more than 4000 m above sea level (Li and Zhou, 1998). Because of its high altitude, it has the highest solar radiation and lowest CO₂ partial pressure of all crop-growing regions on earth. It has been observed that solar radiation even exceeded solar constant on the plateau if the sky is clear and accompanied by some low clouds (Xie, 1983). As solar radiation

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and CO₂ supply energy and mass for photosynthesis, respectively, the importance of their influence on photosynthesis and thereby the productivity of vegetation is very different from that in low plains. Initial photon yield and maximal carboxylation is limited by low CO₂ partial pressure under plateau climate. The $P_n/[CO_2]$ curve is steeper at low [CO₂]. Therefore, plants will give more sensitive response to global change in CO₂ concentration on the plateau than that in low plains. On the other hand, photosynthesis of plant is usually inhibited by high light intensities. Responses of photosynthesis to the combination of these two factors are seldom reported, particularly in the area.

There are many observations on leaf photosynthesis for different varieties of plant. Up to now, it is regularly seen that models describing responses of photosynthesis to individual factors, such as rectangular hyperbola, and one-peaked curve. Such kind of equations can be used to describe empirically the relations between P_n and single factors. The other kind of models is mechanistic ones. One of which is a biochemical model describing biochemical processes of photosynthesis. But they are not capable to simulating responses of photosynthesis to environmental factors because they do not include the stomatal regulation and gaseous diffusion. Under natural conditions, it is necessary to simulate joint effects of environmental factors such as solar radiation, temperature and vapor pressure deficit (VPD), which are interacting with each other in a complex manner, and can be described only by complex mechanistic model. Comprehensive models of photosynthesis which integrate mass transfer, stomatal regulation, biochemical reactions and energy balance have been reported, for example, combined photosynthesis–transpiration–stomatal conductance model (Collatz et al., 1991; Leuning, 1995; Yu and Wang, 1998; Yu et al., 2001). But this kind of models is not easy in use, as the solution of the models needs complex iterations reflecting interactions among physiological and physical processes. Therefore, it is necessary to construct simple physiological models with biological basis. The model should be concise and suitable for use under natural condition, and be

able to describe the processes of photosynthesis in response to environmental factors in the study of crop growth model and interactions between vegetation and atmosphere.

The objectives of this study are to characterize wheat photosynthesis in Tibet, particularly under condition of high irradiance, and then to develop a photosynthesis model which has biological basis to simulate wheat photosynthesis properly both on the plateau and in the plain. Then the model could be applied for calculation of plant productivity on the plateau. As the environment on the plateau is very different from that in low plains, it is helpful to reveal characteristics of ecology to compare the response there with those in the North China Plain.

2. Method

Experiments in Tibet were conducted at Lhasa Agricultural Experiment Station (29°41'N, 91°20'E, 3688 m a.s.l.), Chinese Academy of Sciences, which is near the Lhasa River. Precipitation is rare there during the growing season of winter wheat but enough water is available for irrigation. The area belongs to semi-arid temperate plateau climate zone. Photosynthesis of flag leaves was observed for 5–8 days at each growth stage in 1995 and 1996. The measurements were nearly continually done from sunrise to dusk on each observation day. Data were collected once a minute for each leaf, and only data collected within 10 min were used to avoid the influence of photoinhibition.

Experiments in low plain were conducted at Yucheng Comprehensive Experiment Station (36°57'N, 116°36'E, 28 m a.s.l.), Chinese Academy of Sciences. The rates of photosynthesis and transpiration, and stomatal conductance of winter wheat leaves were measured from tillering stage to maturity (March 29–June 3, 1998). Measurements of leaf physiological variables and various environmental factors were made of a total of 32 days including both clear and cloudy days. Measurements were conducted every 2 h from 8:00 to 18:00 on each observational day. Flag leaves of three plants were used for measurements. The

infrared CO₂ analysis system CI-301PS of CID Co., USA, was used. When intercellular CO₂ concentration calculated (C_i) was lower than 100 $\mu\text{mol mol}^{-1}$, the data set was considered to be unreasonable, and was discarded. The system was calibrated once a week, and showed stable performance. There was ample water and fertilizer supply.

There is a little difference in frequency of examining between the two sites. Observations were conducted every 2 h in a day in the low plain, and nearly continuously in a day on the plateau. Most measurements were made with horizontal leaf surface in the chamber, and some others with different angles with sunbeam to get different light intensities. Regularly, a record was taken within 15 min for each leaf. Solar radiation on the plateau is about 2800 $\text{mol m}^{-2} \text{s}^{-1}$ or more at its maximum around noon. Temperature is relatively low compared with that in low plains. Therefore, growth period of winter wheat lasts from March to early June in the plain, but from April to August on the plateau. The wheat fields were irrigated routinely, according to soil water content. Regularly, irrigation water of about 70–100 mm was flooded three times after turning-green stage. Areas of cultivation were more than 20 hectares.

3. The models

There is a close relation between crop photosynthesis and stomatal conductance. Stomatal opening regulates photosynthesis through the way by influencing the intercellular CO₂ concentration, and thereby the biochemical processes in chloroplast (Yu et al., 2001). The extent of stomatal opening is jointly determined by light intensity and water balance of guard cells, the former involving the reaction of light receptors and the response to intercellular CO₂ concentration, and the latter are conditioned by the water balance of bulk leaf tissue and loss from the guard cells to the immediate aerial environment.

3.1. Stomatal regulation submodel

Ball et al. (1987) proposed a semi-empirical stomatal model in which the mathematical relation between relative humidity over leaf surface (h_s), CO₂ concentration (C_s) and photosynthetic rate (P_n) was represented by the following equation under conditions of ample water supply:

$$g_s = a \frac{P_n h_s}{C_s} + g_0 \quad (1)$$

in which a is a constant, h_s the relative humidity and C_s CO₂ concentration, respectively of air over leaf surface, g_s stomatal conductance, and g_0 a parameter. As there is a positive relation between transpiration rate E_t and VPD from stomatal pore to leaf surface (VPD_s), ($E_t = g_s \text{VPD}_s$), Leuning (1995) revised Ball–Berry model by replacing h_s with VPD_s . When the difference between leaf temperature and air temperature is relatively small compared to diurnal change of those temperatures, VPD_s is close to the VPD in air. Therefore, we use VPD instead of VPD_s because VPD is a meteorological variable and can be easily obtained.

$$g_s = a \frac{P_n}{(C_s - \Gamma)(1 + \text{VPD}/\text{VPD}_0)} + g_0 \quad (2)$$

in which Γ is the CO₂ compensation point, VPD_0 is a parameter reflecting characteristics of response of stomata to atmospheric VPD (Pa).

From flux–gradient relation:

$$C_i = C_s - P_n/g_s \quad (3)$$

where C_i is the intercellular CO₂ concentration. Under weak light, P_n is close to 0, and g_s is also approximately close to 0. From Eq. (2), g_0 is a constant near 0. Therefore, suppose $g_0 = 0$, by combining Eq. (2) and Eq. (3), the following relation holds

$$C_i = C_s - (C_s - \Gamma)(1 + \text{VPD}/\text{VPD}_0)/a \quad (4)$$

This simplified equation is adopted to calculate intercellular CO₂ concentration (C_i) from atmospheric CO₂ concentration and humidity.

3.2. Biochemical submodel

Farquhar et al. (1980) and von Caemmerer and Farquhar (1981) proposed a biochemical model of photosynthesis for C_3 plant, in which photosynthesis is expressed as a function of intercellular CO_2 concentration (C_i), photosynthetic photon flux density (PPFD or I) and temperature (T_i). Collatz et al. (1991) and Leuning (1995) revised the model to simulate the coupling of photosynthesis and transpiration. In this submodel, C_i is taken as an input variable, so it is a biochemical model reflecting reactions in chloroplast excluding stomatal regulation. The relation between photosynthesis and irradiance (I) was expressed as a non-rectangular hyperbola (Thornley, 1976):

$$\theta P^2 - P(\alpha I + P_{\max}) + \alpha I P_{\max} = 0 \quad (5)$$

in which α is initial photochemical efficiency, and P the gross photosynthetic rate.

A reasonable solution of Eq. (5) is

$$P = \frac{\alpha I + P_{\max} - \sqrt{(\alpha I + P_{\max})^2 - 4\theta(\alpha I P_{\max})}}{2\theta} \quad (6)$$

and also $P_n = P - R_d$, in which R_d is dark respiration. The parameters α and P_{\max} relate to biochemical processes which are influenced by environmental factors. They are mainly:

3.2.1. Initial photon efficiency

α is greatly influenced by CO_2 concentration (Goudriaan et al., 1985):

$$\alpha = \alpha_0(P_i - \Gamma)/(P_i + 2\Gamma) \quad (7)$$

in which α_0 is initial quantum efficiency of CO_2 assimilation, and P_i is CO_2 partial pressure, which is given by $P_i = P_0 C_i$. C_i is intercellular CO_2 concentration in mole fraction, and P_0 is the atmospheric pressure.

3.2.2. Maximal photosynthetic rate (P_{\max})

P_{\max} is mainly determined by the activity of Rubisco, and is a function of temperature and CO_2 partial pressure (Collatz et al., 1991)

$$P_{\max 0} = V_m(P_i - \Gamma)/(P_i + C_0) \quad (8)$$

in which, V_m is the maximum catalytic capacity of Rubisco per unit leaf area, C_0 is a parameter

reflecting the Michaelis constants for Rubisco reaction, and is taken here as constant.

V_m depends on temperature (T_a) (Collatz et al., 1991):

$$V_{m0} = V_0 Q_{10}^{(T_a - 25)/10} \quad (9)$$

$$V_m = V_{m0} \{1 + \exp[(-a_1 + b_1 T_a)/(RT_a)]\}^{-1} \quad (10)$$

in which a_1 , b_1 and V_{m0} are parameters, and V_0 is V_{m0} when temperature is 25 °C. R is the universal gas constant.

For plant grown under plateau climate, the light intensity can be so high that there is a range of it in which P_{\max} decreases with an increase in it. The decrease is non-linear, i.e. P_{\max} declines slightly when light intensity is not high, and then after a certain value, P_{\max} declines sharply. There have been some results to support this assumption, i.e. photoinhibition may occur even at low light intensity (Yu et al., 2001). This relation can be described as:

$$P_{\max} = P_{\max 0} \{1 - \exp[k(I/I_0 - 1)]\} \quad (11)$$

in which, k is a parameter characterizing the relative rate of decrease, and I_0 the maximal light intensity under which photosynthetic rate achieves 0. Fig. 1 shows the calculated decrease in P_{\max} in response to increasing light intensity according to Eq. (11) which is a non-linear curve.

In the plain, where the decrease in photosynthetic rate is weak, no corrections need be made in using the equation with a plateau, i.e. $P_{\max} = P_{\max 0}$.

3.2.3. Dark respiration (R_d) is proportional to V_m (Collatz et al., 1991)

$$R_d = k V_m \quad (12)$$

In conclusion, the models consist of Eq. (4) and Eqs. (6)–(12). This simplified photosynthesis model can be divided into two parts: (1) based on stomatal model, relation between intercellular CO_2 concentration (C_i) and atmospheric CO_2 concentration and atmospheric humidity is derived, i.e. $C_i = f(C_s, VPD)$; (2) according to the biochemical model, the relation between photosynthetic rate and light intensity, temperature and C_i is developed, i.e. $P_n = f(I, T_a, C_i)$.

The input variables of the model are light intensity, temperature, VPD, CO₂ concentration and atmospheric pressure. The photosynthetic rate in Eq. (6) can be obtained directly. In detail, firstly, C_i is obtained from Eq. (4), α from Eq. (7), P_{\max} from Eqs. (8)–(11), and R_d from Eq. (12), and then the obtained values of the variables can be used to substitute for these in Eq. (6), and solve it to get the photosynthetic rate. If stomatal conductance is needed, it can be derived from Eq. (2).

4. Results

4.1. Responses of photosynthetic rate to solar radiation and temperature

4.1.1. Light responses of photosynthesis on the plateau

Solar radiation on the plateau is much higher than that in the plain with humid climate where the PPFD rarely exceeds 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Light response curves of photosynthesis were fitted by the data collected from specific leaf

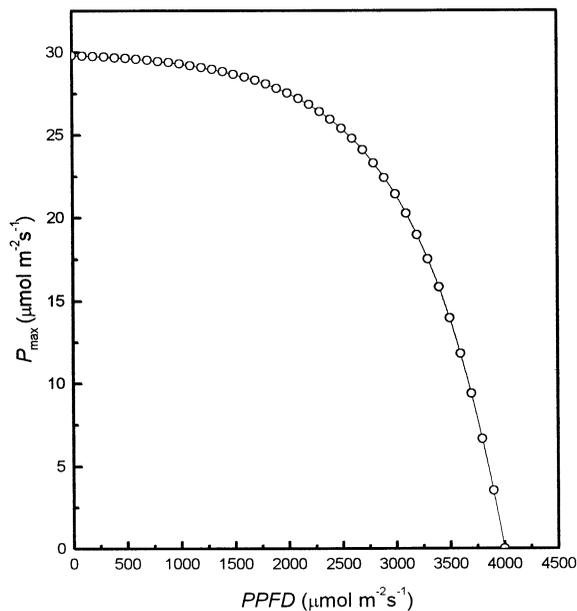


Fig. 1. Assumption of decrease in maximum photosynthetic rate (P_{\max}) with an increase in light intensity ($I_0 = 4000 \mu\text{mol m}^{-2} \text{s}^{-1}$, $k = 5.0$, $P_{\max} = 30 \mu\text{mol m}^{-2} \text{s}^{-1}$).

under stable environmental factors except light intensity. The light response curves obtained from data collected at different time were different from each other. Fig. 2 shows two typical light response curves of photosynthesis of wheat in Tibet in a given time period (similar figures were omitted). It indicated that other environmental factors influence significantly photosynthesis, or more precisely, the parameters in response curves of photosynthesis.

Fig. 3 shows a typical light response of wheat in Tibet, in which photosynthetic rate was observed under different atmospheric conditions of temperature, humidity and CO₂ partial pressure in days. All light curves display similar features. It can be seen that photosynthetic rate keeps at its maximum value within the range of PPFD from 900 to 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and shows a distinct decrease beyond 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. At low light levels, photosynthetic rate is approximately a linear function of irradiance.

As high light intensity may cause photoinhibition of photosynthesis or photooxidation of some important components of the photosynthetic apparatus, leaf photosynthetic rate decreases with time under exposure to high irradiance on the plateau. Fig. 3 shows a continuous measurement of photosynthesis for a leaf under solar radiation higher than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with an average value of 1720 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The decrease was linear with time up to 80 min. The scatter of points in fitting the light–photosynthesis curve is more conspicuous than that in the plain, which may be ascribed to marked decrease in photosynthetic rate with time under high irradiance.

4.1.2. Temperature response of photosynthesis in Tibet

An alternative approach, used by Cheeseman et al. (1991), was based on the collection and analysis of a large data set under uncontrolled field conditions. Fig. 3 shows the simulated response curves to temperature and irradiance. The data were collected under different temperature, radiation and humidity conditions, which illustrated that it was hard to predict by models of a single factor the behavior of all leaves exactly even when they seem to be quite similar. It can be seen from

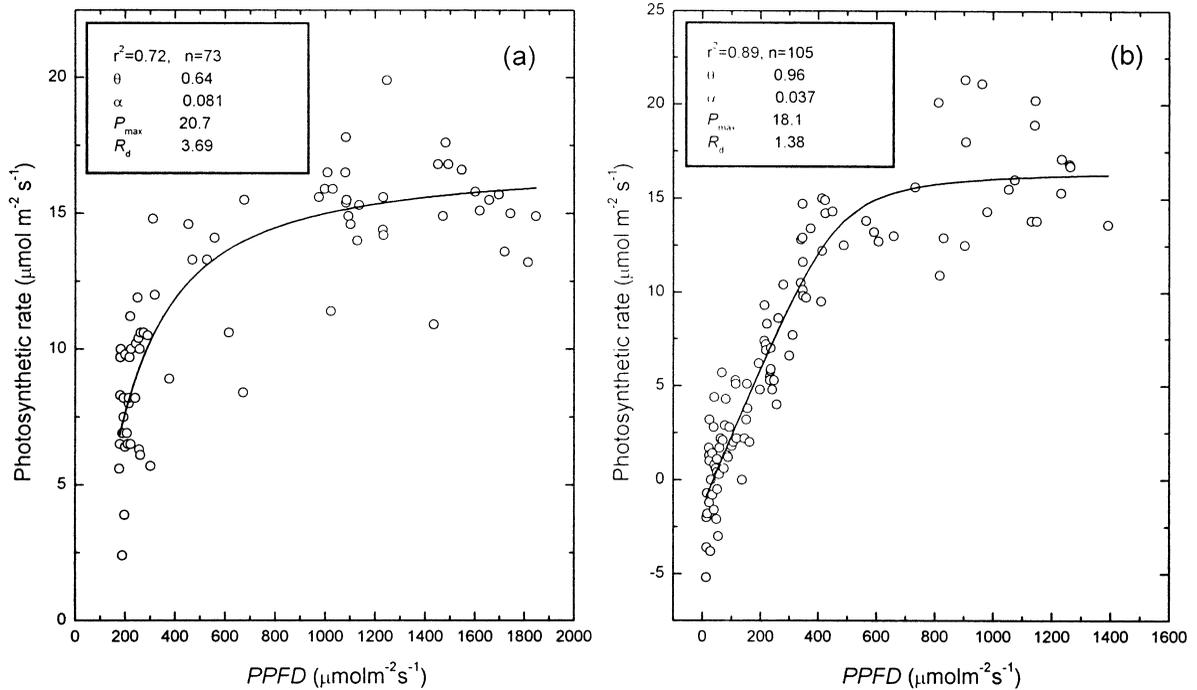


Fig. 2. Responses of photosynthesis of flag leaves to PPFD at different time on the Tibetan Plateau (Lhasa, (a) 17:45–18:56, July 17 and (b) 15:47–17:01, July 24, 1996).

the spread of points in Fig. 3b, d, and f that there is an envelope around the points showing limitation of photosynthesis by temperature when other factors are suitable. Therefore, from the envelope of points one can see that the optimum temperature of photosynthesis is about 25–27 °C. Photosynthetic rate decreases sharply with marked stomatal closure (figures omitted) in Tibet when temperature rose from 33 to 36 °C, and optimal temperature is not far from the maximal temperature of photosynthesis (Fig. 3).

Temperature on the plateau changes over a wide range (from 15 to 36 °C) in a day, under which the plotting of wheat photosynthesis against temperature shows a marked optimum. Often not well-defined photosynthesis–temperature relations can be seen in the plain. It may be ascribed to small variation of temperature in the plain.

4.1.3. Light response of photosynthetic rate in the plain

It is helpful to compare the light response curves of P_n in the plain and on the plateau. When photosynthetic rates and light intensity in the field are fitted by a non-rectangular hyperbola (Fig. 4), a good relation is obtained. The initial slope of the fitted curve (α) is 0.068. For well-grown crops, α is far lower than its theoretical maximum (0.08), it generally ranges from 0.04 to 0.07 under field conditions (Xu et al., 1984). P_{max} is 23.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is basically the photosynthetic rate at saturation point of light (Fig. 4).

As temperature ranges frequently from 20 to 32 °C in May in this area, its influence on diurnal variation of photosynthesis is not so evident as that of solar radiation that changes from zero to a value exceeding light saturation point.

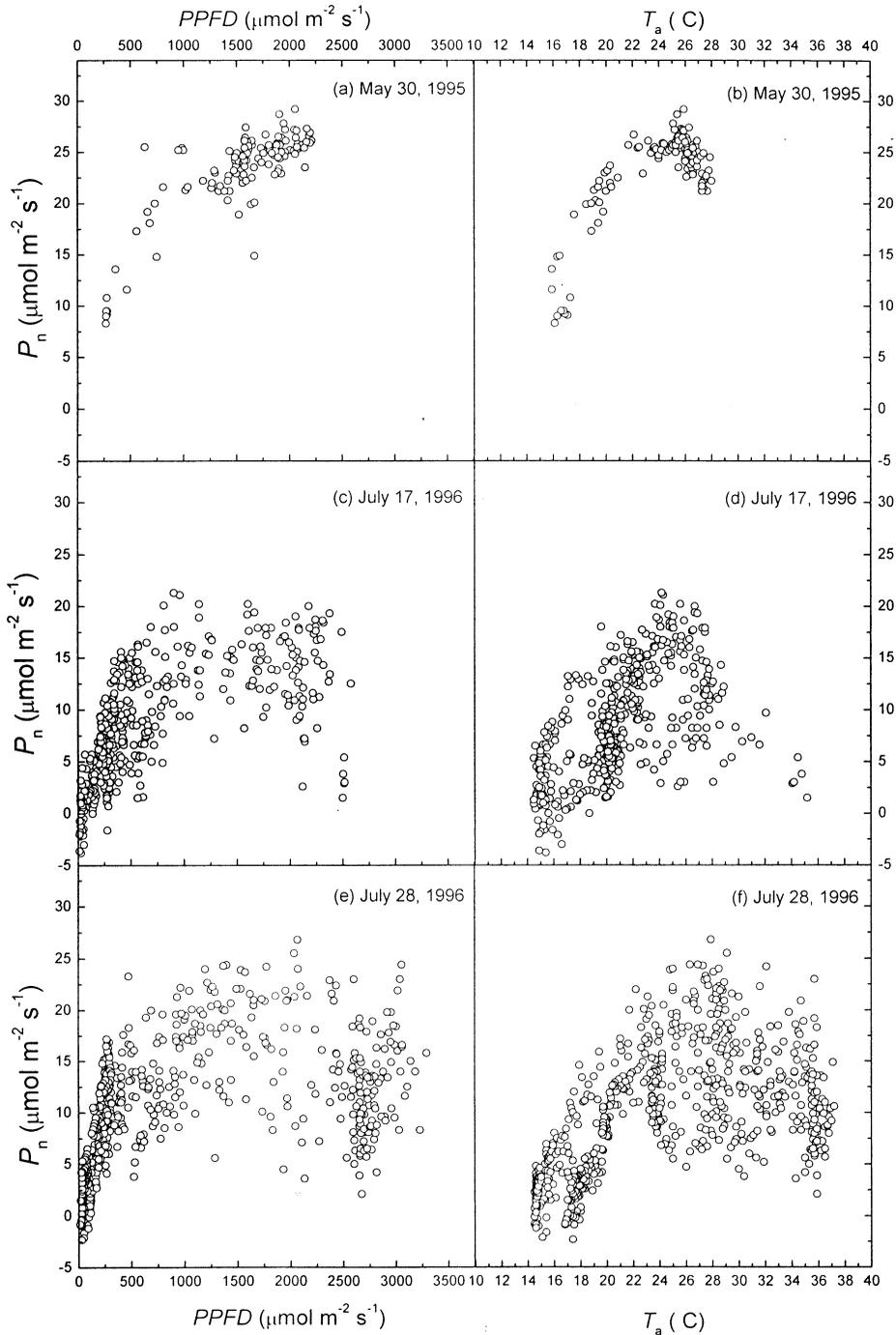


Fig. 3. Responses of photosynthesis of flag leaves to PPFD and temperature of 3 days on the Tibetan Plateau (Lhasa, May 30, 1995; July 17, 1996; July 28, 1996).

4.2. Simulation of the dependence of photosynthetic rate on environmental factors

4.2.1. Sensitivity of the model to environment

Dependence of photosynthetic rate on irradiance, temperature, VPD and CO₂ concentration is calculated, respectively to estimate the sensitivity of the model to certain environmental factors, by holding other factors unchanged. Fig. 4 is the calculated result with the given values of parameters. The response curve of photosynthetic rate to light intensity is a typical Michaelis–Menten curve (Fig. 5a), and the response to temperature is a one-peaked curve with an optimum at about 26 °C (Fig. 5b). When water vapor pressure in air decreases, leaf transpiration will be enhanced, which causes stronger water loss of guard cells and thereby causes a decrease in stomatal conductance, which in turn lowers intercellular CO₂ concentration, and thereby the photosynthetic rate (Fig. 5c). Relative humidity and water vapor

pressure are physical variables reflecting atmospheric humidity, and there is certain conversion relation of them. Increase in CO₂ concentration will induce elevation in intercellular CO₂, and the increase in photosynthetic rate (Fig. 5d). These results of simulations accord well with these of many experiments.

4.2.2. Model verification

The model was run with observational data of meteorological variables as inputs. After the CO₂ compensation point is given, VPD₀ is adjusted so that the relation between simulated and measured P_n achieves the highest coefficient of correlation, which is taken as the best fit. Outputs of the simulated photosynthetic rates were compared with their measured values.

In the plain, according to some studies (Collatz et al., 1991; Leuning, 1995; Lu et al., 2000), the parameters used are as follows: $V_0 = 55.0 \text{ mol m}^{-2} \text{ s}^{-1}$, $Q_{10} = 2.4$, $k = 0.034$, $a_1 = 220.0 \text{ kJ mol}^{-1}$, $b_1 = 703.0 \text{ J mol}^{-1} \text{ K}^{-1}$, $R = 8.314 \text{ J mol}^{-1} \text{ K}^{-1}$, VPD₀ = 1500.0 Pa, $G = 5.0 \text{ Pa}$, $C_0 = 8.0 \text{ Pa}$, $a_0 = 0.08$, $\theta = 0.90$, $P_0 = 1005.0 \text{ hPa}$, $\theta = 0.55$. For Tibet, for most of parameters the same values as used in the plain were used except that $V_0 = 68 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $\theta = 0.55$. Atmospheric pressure at Lhasa is about 2/3 of that in the plain (Li and Zhou, 1998).

Fig. 6 and Fig. 7 are comparisons of simulated and measured photosynthetic rates in the plain and on the plateau, respectively. It can be seen that the simulated values in the plain correspond well with the measured ones, with points distributed around the 1:1 line (Fig. 6). A good linear relation of simulated and measured values has been obtained, with a slope of 0.991, very close to 1, and the intercept in Y-axis of simulated P_n is -0.036 , very close to 0, which shows that the model simulates leaf photosynthesis quite well. Agreement of simulated and observed photosynthetic rates on the plateau is also good, but spread of points is slightly greater than that obtained from the plain.

The validation of the model to diurnal variation of photosynthetic rate under consideration of declination of P_{max} and not.

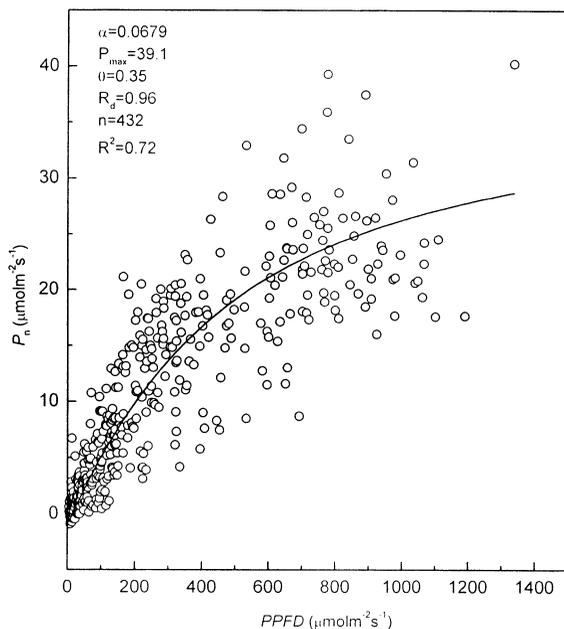


Fig. 4. Light response of leaf photosynthesis of winter wheat in the North China Plain (Yucheng, measured every 2 h from 8:00 to 18:00 in a total of 32 days in the growth season).

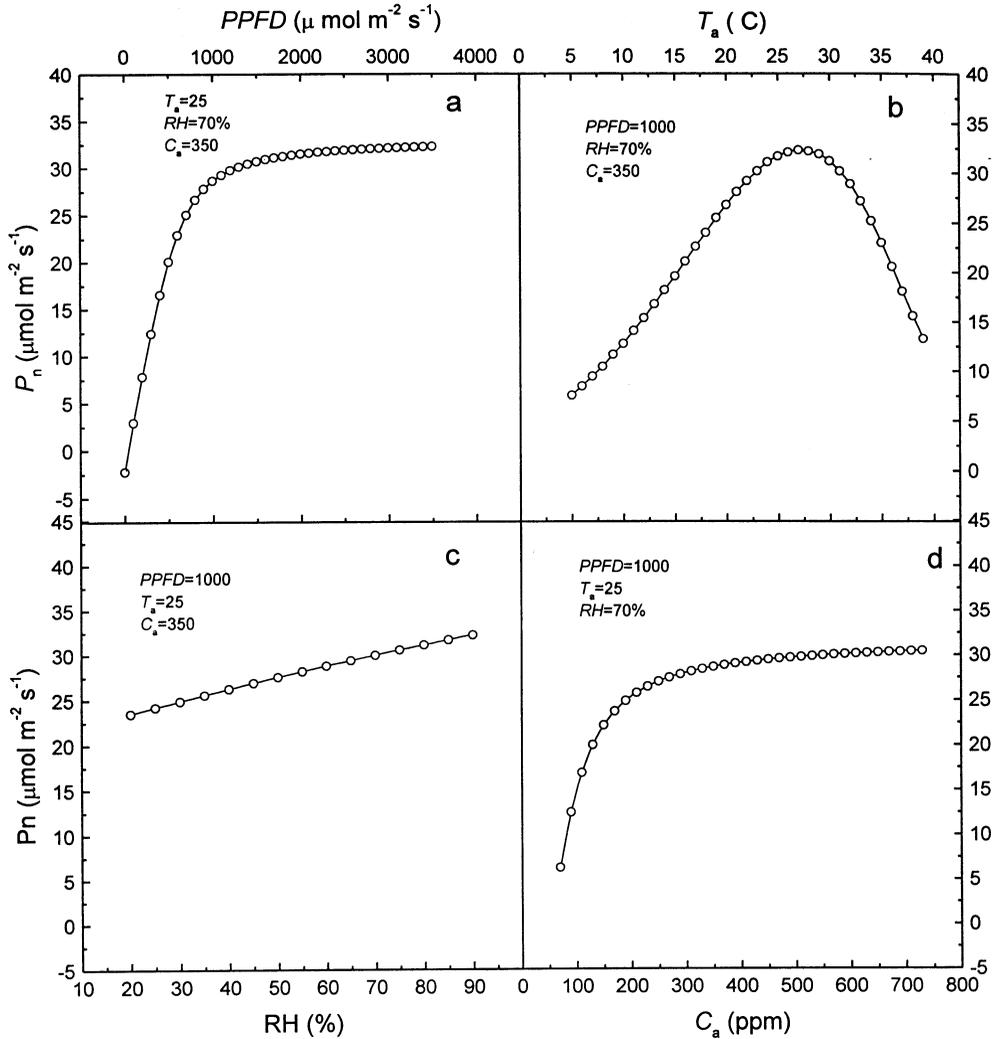


Fig. 5. Responses of photosynthesis to changes of environmental factors simulated by the physiological model (PPFD: photon flux density, T_a : temperature, RH: relative humidity, C_a : CO_2 concentration).

5. Discussion

When leaves are exposed to high light, the proportion of absorbed light energy dissipated through non-radiative processes (as heat) at the photosystem II (PSII) antennae increases and, consequently, the quantum efficiencies of PSII photochemistry and CO_2 assimilation decrease (Baker, 1991). The excess of light can inhibit photosynthesis which can be detected as a decrease in P_{max} and may lead to photooxidative

impairment of the photosynthetic apparatus (Long et al., 1994; Demmig-Adams and Adams, 1992). Photoinhibition of photosynthesis by light of high intensity will consequently lower CO_2 uptake and accumulation of dry matter.

The climate in Tibet is unique in its high solar radiation and low CO_2 partial pressure. The light response curve in Tibet is not a hyperbola, as photosynthetic rate decreases with the increase in light intensity beyond certain limit. Hence, the productivity of vegetation in Tibet may be overes-

timated if the lowering of photosynthesis under high light is not taken into account.

The photosynthesis model based on biochemical processes is widely used, at levels from leaf, canopy up to global (Wirtz, 2000; Yu et al., 2001; Liu De Li, 2002; Pachepsky and Acock, 2002). There is small difference among such kind of models. The main difference is mathematical description of parameters in the equation. Here a small improvement is made by considering the possible decline of P_{\max} with an increase in solar radiation in order to make the kind of model applicable for plateau climate. Because the regular non-rectangular photosynthetic response curve will overestimate photosynthetic rate on plateau when solar radiation is high.

Diurnal changes in temperature are very large in Tibet, as solar radiation is high in daytime and greenhouse effect of atmosphere at night is very weak due to the thin air. The large range of diurnal changes of temperature between 12 and 36 °C on the Tibetan Plateau have marked effect on photosynthesis, in contrast to between 22 and 36 °C in the plain at the middle latitude. There-

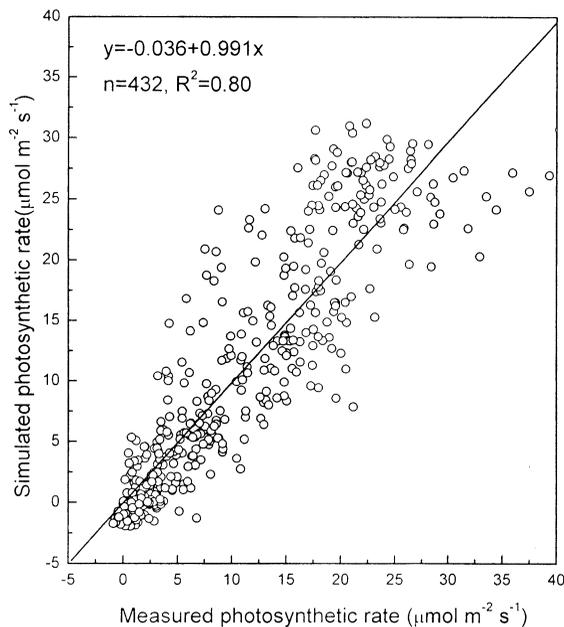


Fig. 6. Comparison of simulated and observed photosynthetic rates in the North China Plain (Yucheng, 1998).

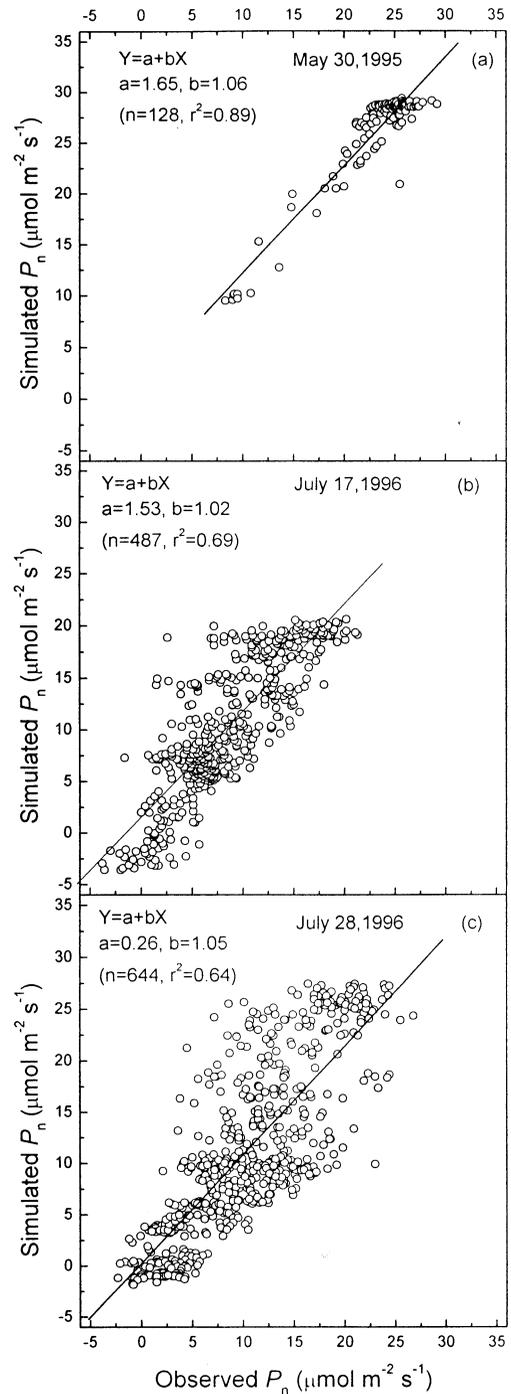


Fig. 7. Comparison of simulated and observed photosynthetic rate on the Tibetan Plateau (Lhasa, May 30, 1995; July 17, 1996; July 28, 1996).

fore, temperature also shows a more pronounced on diurnal courses of photosynthesis. As leaf chamber will be warmed greatly by high solar radiation, photosynthetic rate falls, and it is advisable to take measurement of photosynthesis within 10 min.

Parameters of light response curve of photosynthesis may be different for different areas or development stages in a variety of plant. For example, maximum carboxylation rate determined by enzyme activity is sometimes assumed to be a linear function of nitrogen content of leaf (Leuning, 1995). In verification of the model, some parameters are pre-given which still need some measurements by critical experiment in future study. The generality of the model may be expanded if more factors affecting P_n are included, such as leaf water potential.

The many physical and physiological processes are interacting with each other. It is one of the basic tasks of physiological ecology to parameterize the processes and develop comprehensive model. But under natural conditions, the magnitude of contribution of changes in each environmental factor to variations in assimilation may vary widely and some factors and processes are dominant under a particular circumstance and may have little effect under others (Leverenz, 1994). For example, solar radiation changes from zero to more than photosynthetic saturation point in a day. When water stress is not extremely serious, diurnal variation of photosynthesis is dominated by solar radiation. Therefore, the physiological model of photosynthesis, in this study Eq. (6), uses light response curve as the core of the model, whereas the other factors exert their influence by affecting the values of some parameters in the model. A key resolution is parameterization of C_i , which is based on some observational data and stomatal models.

Besides the factors considered in the model, such as irradiance, temperature, humidity and CO_2 , the influence of boundary layer resistance on photosynthesis can be significant when wind speed is very low (Collatz et al., 1991). In a leaf chamber, wind speed over leaf surface is high and boundary layer conductance could be neglected. Under natural conditions, the changes in C_i

caused by changes in boundary layer conductance could also be neglected on the ground that its influence on photosynthesis is small under most conditions. To include influence of wind speed in the model under natural conditions, gaseous diffusion equation may be considered to calculate leaf surface CO_2 and humidity.

Compared to experiments conducted in laboratory, there is a wider scattering of points in figures of data collected from measurements in the field versus simulation. Occasionally, the changing environment in the field results in fluctuation of input of the observational system, and then magnify error of the record due to frequent response of the system to the change. In addition, photosynthetic system and parameters in the model change with development stage (Lu et al., 2000).

Although the model could respond to changes in CO_2 , and temperature, as well as solar radiation, the long-term acclimation of photosynthesis system can be integrated into the short-term response. Therefore, it is possible to evaluate the influence of climate change, such as increase in CO_2 in atmosphere and global warming, especially for plants under plateau climate with high solar radiation.

This study analyzed primarily the response of photosynthesis to high solar radiation, low CO_2 pressure, and large variation in temperature on Tibet Plateau. The mechanism of responses photosystem to these regimes, for example, the photoinhibition under plateau climate and characteristic parameters of light response curves, i.e. initial photon yield, and maximum photosynthetic rate are essential for the evaluation of the primary production of the specific region. Research in these fields need to be enhanced in the future.

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