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Modelling diurnal courses of photosynthesis and transpiration of leaves on the basis of stomatal and non-stomatal responses, including photoinhibition

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Abstract

A mathematical model for photoinhibition of leaf photosynthesis was developed by formalising the assumptions that (*1*) the rate of photoinhibition is proportional to irradiance; and (*2*) the rate of recovery, derived from the formulae for a pseudo first-order process, is proportional to the extent of inhibition. The photoinhibition model to calculate initial photo yield is integrated into a photosynthesis-stomatal conductance (g_s) model that combines net photosynthetic rate (P_N), transpiration rate (E), and g_s, and also the leaf energy balance. The model was run to simulate the diurnal courses of P_N, E, g_s, photochemical efficiency, *i.e.*, ratio of intercellular CO_2 concentration and CO_2 concentration over leaf surface (C_i/C_s), and leaf temperature (T_l) under different irradiances, air temperature, and humidity separately with fixed time courses of others. When midday depression occurred under high temperature, g_s decreased the most and E the least. The duration of midday depression of g_s was the longest and that in E the shortest. E increased with increasing vapour pressure deficit (VPD) initially, but when VPD exceeded a certain value, it decreased with increasing VPD; this was caused by a rapid decrease in g_s. When air temperature exceeded a certain value, an increase in solar irradiance raised T_l and the degree of midday depression. High solar radiation caused large decrease in initial photon efficiency (α). P_N, E, and g_s showed reasonable decreases under conditions causing photoinhibtion compared with non-photoinhibition condition under high irradiance. The T_l under photoinhibition was higher than that under non-photoinhibition conditions, which was evident under high solar irradiance around noon. The decrease in C_i/C_s at midday implies that stomatal closure is a factor causing midday depression of photosynthesis.

Additional key words: diurnal courses; initial photon efficiency; irradiance; leaf temperature; midday deppression; model; photosynthetic photon flux density; stomatal conductance; temperature.

Introduction

Irradiation of leaves in excess of what can be utilised in photosynthesis may result in photoinhibition that is manifested as a decline in maximal quantum efficiency of photosynthesis, α (Powles 1984, Long *et al.* 1994). Many studies were done on various aspects of photoinhibition using biophysical, biochemical, and physiological methods (for detailed reviews, see Powles 1984, Demmig-Adams and Adams 1992, Long *et al.* 1994), but only few works have been done to integrate the experimental results by using mathematical tools. In many models of photosynthesis, α is introduced as a constant (Hall 1979, Johnson and Thornley 1984, Harley *et al* 1992), or changes only with leaf temperature and CO_2 noccentration (Goudriaan *et al.* 1985, Harley and Tenhunen 1991, Cannell and Thornley 1998). However, α may decrease significantly on clear days with no other stress. The diurnal changes in α and the convexity (θ) of the non-rectangular hyperbola used to describe irradiance

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response curves of photosynthesis, can be estimated from the extent of decrease of F_v/F_m as a function of irradiance By providing measured irradiance as an input into the photon response function, daily P_N was calculated to decrease by 13 % by photoinhibition, even with no other stress (Ögren and Sjöstrom 1990). However, in nature photoinhibition is often accompanied by other stresses, such as drought (Xu and Shen 1997), under which P_N may be overestimated if photoinhibition is not considered.

The leaf level is the basic level in physiological ecology, as observation values are easy to obtain using infrared gas analyser, and so leaf physiological models are better worked out than those at higher levels. Canopy models are obtained by scaling up the leaf level model. The daily course of physiological responses is also a basic level in terms of time scale (Jarvis 1995). There are some observations of daily courses and midday depressions of P_N and E under photoinhibition (Barták *et al.* 1999, Muraoka *et al.* 2000). Their simulations are less studied, except that Collatz *et al.* (1991) simulated the influence of laminar boundary layer conductance on the midday depression of P_N and E. The influence of photoinhibition on daily courses of P_N is closely correlated with environmental factors, but it is difficult to reveal its extent by experimental method (Fig. 4 in Long *et al.* 1994).

To simulate physiological responses of the plant leaf to the environment, a semi-empirical model proposed by Ball *et al.* (1987) summarised the relation between g_s and an index relating P_N of a leaf, relative humidity, and CO_2 concentration over the leaf surface with a linear equation (hereafter referred to as BWB model). Since g_s and P_N are interdependent, the solution of the BWB model needs a photosynthesis sub-model. Therefore Leuning (1990) proposed to solve a combined P_N-g_s model. By combining the BWB model with Farquhar's biochemical model of photosynthesis, Collatz *et al.* (1991) proposed that boundary layer conductance (g_b) over a leaf surface may cause midday depression, and both too large or too small value of g_b will cause a decrease in photosynthesis (Schuepp 1993). But Fu and Wang (1994) found that the relation between g_s and g_s index ($P_N h_s/C_s$) will change when g_b changes, which implies that there may be a better index reflecting relation between g_s and its response to ambient CO_2 concentration and humidity. Since many studies reveal that stomata respond to VPD in a better-defined way than to relative humidity (h_s), Leuning (1995) revised the BWB model using VPD as evaporative demand instead of h_s. Aphalo and Jarvis (1993) studied effects of g_b on gas transfer, and constructed a mathematical relation among vapour pressure deficit from stomatal pore to leaf surface (VPD_s), g_b, and g_s by using gaseous diffusion equation. By incorporating the equation of Aphalo and Jarvis (1993) into the P_N-g_s model (Collatz *et al.* 1991, Leuning 1995), Yu and Wang (1998) give a more realistic simulation of stomatal responses to changes in g_b.

The objectives of this study are: (*1*) to incorporate the photoinhibition model into the integrated P_N-E-g_s model for its use in the analysis of midday depression; (*2*) to evaluate the influence of stomatal and non-stomatal factors in a plant leaf on diurnal variation of P_N and E under changing environment, especially under conditions leading to a midday depression.

The model

The model combines the P_N-g_s sub-model proposed by Collatz *et al.* (1991), a revised version of the BWB stomatal model, and a sub-model of E based on gaseous transfer processes proposed by Aphalo and Jarvis (1993), and finally a newly proposed photoinhibition model.

Stomatal conductance submodel: Goudriaan and van Laar (1978) and Wong *et al.* (1979) found that under steady state conditions, there is a linear relation between stomatal conductance to CO_2 (g_{sc}) and P_N under changing of some environmental variables, such as irradiance, on which the BWB stomatal model is based:

$$g_{sc} = \mathrm{m}\frac{P_N h_s}{C_s} + \mathrm{b} \tag{1a}$$

where h_s 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 co-ordinate of g_{sc} near zero. $P_N h_s/C_s$ is referred to as stomatal conductance index. Seeing that Eq. 1a is not applicable to low CO_2 concentrations, Leuning (1990) found that using C_s-Γ, where Γ is the CO_2 compensation concentration, instead of C_s gave a better fit. Experiments revealed that stomata respond to evaporative demand (VPD_s) more than to relative humidity of air (Sheriff 1984, Grantz and Zeiger 1986, Grantz 1990, Mott and Parkhurst 1991). By adopting these modifications, Leuning (1995) proposed a revised form of the BWB model:

$$g_{sc} = \mathrm{m}\frac{P_N}{(C_s - \Gamma)(1 + \mathrm{VPD_s}/\mathrm{VPD_0})} + g_{s0} \tag{1b}$$

where g_{s0} is equivalent to the parameter b in Eq. 1a, and VPD_0 is a parameter characterising the curve of response of g_s to VPD_s.

Here we propose that gross assimilation rate (P_G) should be used instead of P_N, as g_s begins to increase immediately with increasing irradiance, even below the compensation irradiance:

$$g_{sc} = \mathrm{m}\frac{P_g}{(C_s - \Gamma)(1 + \mathrm{VPD_s}/\mathrm{VPD_0})} + g_{s0} \tag{1c}$$

Photosynthesis sub-model: The biochemical model of Farquhar *et al.* (1980) generalises the main aspects of intercellular biochemical processes. One of the input factors needed is intercellular CO_2 concentration, which in turn is determined by P_N and g_s. Since g_s and P_N sub-models are interdependent, they must be used in combination by iteration to predict physiological responses to changes in environmental factors. The model used here is the one proposed by Farquhar *et al.* (1980) and Caemmerer and Farquhar (1981). The equations and parameters used here are from Collatz *et al.* (1991). P_G may be described as

$$P_G = \min\{J_e, J_c, J_s\} \qquad (2)$$

where J_c and J_e are the gross rates of photosynthesis limited by carboxylation reaction catalysed by ribulose-1,5-bisphosphate carboxylase/oxygenase and by the rate of ribulose-1,5-bisphosphate (RuP_2) regeneration limited by the rate of electron transport supported by radiant energy received, respectively. J_c depends on intercellular CO_2 concentration (C_i) and temperature. J_e depends not only on C_i and temperature, but also on irradiance. J_s is the capacity for the export or utilisation of photosynthates.

Transpiration sub-model: Stomata are sensitive to both CO_2 and water vapour concentrations, with their aperture enlarging as CO_2 concentration or VPD decrease. Under natural conditions, the variations of g_b due to wind speed must always be taken into consideration. When g_b is low, the difference between e_a and e_s, the vapour pressure at ambient air and leaf surface, may not be negligible, and a similar situation occurs also with C_a and C_s. Taking this into consideration, Aphalo and Jarvis (1993) derived an expression of VPD_s as a function of VPD_a (the VPD in the ambient air), g_{sw} and g_{bw} (the conductance of stomata and boundary layer to water vapour) as follows:

$$VPD_s = [VPD_a + s(T_l - T_a)]\,(1 - g_{tw}/g_{bw}) \qquad (3)$$

where g_{tw} is overall conductance (g_{sw}+g_{bw}) to water vapour [mol m^{-2} s^{-1}], T_l and T_a are temperatures of leaf and air, respectively, and s is the slope of the saturated water vapour pressure/leaf temperature curve. The calculation of saturated vapour pressure and s can be found in energy balance sub-model. Eq. 3 is derived from the equation for E, in which VPD_s represents the driving force for transpiration.

This relation is derived from mass flux equation for steady state. We have also the relation between g_{sw} and overall conductance in terms of g_{sc} and g_{bw}. By using diffusion equation in steady state, intermediate variables C_s and C_i are expressed as functions of C_a, P_N, and conductance in each part for CO_2.

Photoinhibition sub-model: The primary site of photoinhibition is in photosystem (PS) 2 (Powles 1984). When photoinhibition occurs, maximum quantum use efficiency of PS2 always decreases. The extent of photoinhibition increases with photosynthetic photon flux density (PPFD). Assuming that the rate of change in α_t with time (t) is proportional to the amount of radiant energy absorbed, the following equation holds:

$$d\alpha_t/dt = -K_i\ \mathrm{PPFD} \qquad (4)$$

in which K_i (>0) is the photoinhibition coefficient.

Fluorescence ratio (F_v/F_m) is a good measurement of α, and the change in F_v/F_m in leaves is an index of photoinhibition. There is a linear relationship between F_v/F_m and α (Greer *et al.* 1986, Demmig and Björkman 1987, Demmig-Adams *et al.* 1989, Kao and Forseth 1992, Edwards and Baker 1993). The rate of recovery of photoinhibition can be derived from the formulae for a pseudo first-order process of F_v/F_m (Greer and Laing 1988):

$$d\alpha_t/dt = K_r(\alpha_n - \alpha_t) \qquad (5)$$

in which K_r is the recovery coefficient. Leaf photoinhibition and its recovery occur at the same time. By combining the two components of inhibition and recovery in Eqs. 4 and 5, we have:

$$d\alpha_t/dt = K_r(\alpha_n - \alpha_t) - K_i\ \mathrm{PPFD} \qquad (6)$$

where α_t is α at time t, α_n is the maximal value of α after recovery.

The recovery of photosynthesis from photoinhibition is temperature-dependent with little or no recovery occurring below 15 °C and maximum recovery at 30 °C (Greer *et al.* 1986, 1988). A one-peaked equation is used to simulate the temperature response curve in the paper of Greer *et al.* (1986).

$$K_r = \frac{K_0 \exp[(H_k/RT_0)(1 - T_0/T)]}{1 + \exp[(S_k T - H_d)/(RT)]} \qquad (7)$$

in which parameters $K_0 = 0.0001\ s^{-1}$, $H_k = 79\,500$ J mol^{-1}, $S_k = 650$ J $mol^{-1} K^{-1}$, and $H_d = 199$ KJ mol^{-1}. R is the universal gas constant. T_0 is the reference temperature, $T_0 = 293.2$ K.

To solve Eq. 6, the initial value of α when $t = 0$, *i.e.*, α_0, K_i and K_r are needed. In this study, $\alpha_0 = 0.08$ mol(CO_2)/mol(quantum), and $K_i = 0.21 \times 10^{-8}$ μmol^{-1} m^{-2}.

Energy balance sub-model: Leaf temperature is determined by energy balance, which can be described as (Paw U 1987):

$$R_i = \rho C_p(T_l - T_a)/r_b + \rho C_p[e_s(T_l) - e_a]/[\gamma(r_b + r_s)] + \varepsilon\sigma T_l^4 \qquad (8)$$

where R_i is the leaf absorption of short-wave and long-wave radiation, ρ is air density, C_p the specific heat of air under constant pressure, γ the psychrometric constant, r_b and r_s the boundary layer resistance and stomatal resistance, respectively, ε leaf emissivity (0.95), and σ the Stefan-Boltzmann constant.

$$R_i = aQ + b\sigma T_e^4 \qquad (9)$$

in which Q is solar irradiance [W m^{-2}], a and b are leaf absorptances for short-wave and long-wave radiation, respectively (0.66 and 0.95). Sky long-wave radiation is calculated by sky temperature T_e, an effective temperature related to air temperature (Monteith 1973):

$$T_e = 1.06\,T_a - 21 \qquad (10)$$

When stomatal resistance is given, Eq. 8 can be resolved as:

$$T_l = T_a + \{R_i - \varepsilon\sigma T_a^4 - h_e\,[e_s(T_a) - e_a]\}/(4\,\varepsilon\delta T_a^3 + h_t + h_e s) \qquad (11)$$

Saturated water vapour pressure, $e_s(T_a)$, depends on temperature, and is calculated by the Goff-Gratch equation, with a slope with temperature as s:

$$s = \frac{de_s(T_a)}{dT_a} \qquad (12)$$

where h_e is water transfer coefficient,

$$h_e = \rho C_p/(\gamma(r_b + r_s)) \qquad (13)$$

and h_t is heat transfer coefficient,

$$h_t = \rho C_p/r_b \qquad (14)$$

Numerical solution: Non-linear and complete equations of (1c)-(14) are about unknown numbers of A_g, E_t, g_{sc}, g_{sw}, g_{tc}, g_{tw}, C_i, C_s, VPD$_s$, *etc.* Of these equations, the detailed form of Eq. 2 can be found in the Appendix from Collatz *et al.* (1991). The photoinhibition model is dynamic, and is resolved by Runge-Kutta method. This set of models is used to get the values of iterative method when environmental elements, *i.e.*, solar radiation, T_a, air vapour pressure, C_a, and wind speed or g_b are input. This method is similar to that of Collatz *et al.* (1991). Firstly, a value of T_l is given to calculate α in the photoinhibition model, and then to resolve the P_N-g_s model, *i.e.*, to find a value of C_i, obtain P_N from Eq. 2, and then g_{sc} and a new C_i are obtained. Using the new C_i as the input value, repeat the process until C_i has converged. From the value of g_{sc} obtained we can get a new T_l by resolving leaf energy balance model. When the outer iteration reaches convergence, *i.e.*, the difference in T_l between two steps is less than a small value, the set of physiological variables, P_N, E, g_s, C_i, and α, is taken as the result.

The values of some parameters in the photosynthesis sub-model and g_s sub-model are taken from Collatz *et al.* (1991) and Leuning (1995). In the g_s model, VPD$_0$ = 1 500(Pa), m = 20.

Results

Physiological responses of plant to environmental factors: For convenience of analysis, dependence of P_N, E, and g_s on T_l was simulated under different irradiances in steady state. In Fig. 1, the dependence of g_s on temperature is one with a peak (Jarvis 1980) like the responses of many other biological processes. The optimum temperature of g_s is lower than that of P_N. Although g_s is proportional to P_N under certain conditions (Wong *et al.* 1985a,b,c), an increase in temperature will cause an exponential increase in VPD which will make g_s decline hyperbolically. Thus the magnitude of decline in g_{sc} is greater than those in P_N and E. When T_l is lower than the optimum temperature for g_s, E increases gradually with increasing T_l, because both VPD$_s$ and g_{sw}, the two factors determining E, are affected by an increasing temperature in positive ways. When T_l exceeds slightly the optimum value for g_s, the effect of the increase in VPD$_s$ overruns the effect of the lowering of g_{sw}, and E will continue to increase. When T_l rises further, a point will eventually be reached when the stomata close due to depression of photosynthesis so tightly that E decreases despite the very large VPD$_s$.

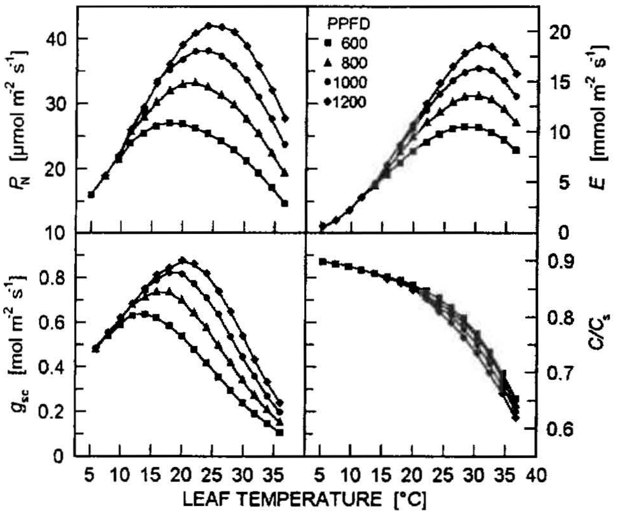

Fig. 1. Changes of net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance for CO$_2$ (g_{sc}) with leaf temperature under different photosynthetic photon flux densities (PPFD).

Next, the photoinhibition sub-model was used to simulate the time courses of photoinhibition of initial quantum yield under PPFDs and its recovery in the dark (Fig. 2). This situation represents laboratory conditions in which other elements are held constant. α decreased sharply in the first two hours, then decreased slowly, and, after 4 h of irradiation, remained almost constant. High irradiances caused rapid decrease in α initially but α held nearly constant after 6 h of inhibition. The recovery rate in the dark was high at first or after strong photoinhibition, and reached nearly the same value as before the inhibition. Such phenomenon has been observed many times in experiments in laboratories (Powles and Björkman 1982, Greer *et al.* 1986, Demmig and Björkman 1987, Ögren 1991, Ottander and Öquist 1991, Kao and Forseth 1992, Tyystjärvi *et al.* 1994).

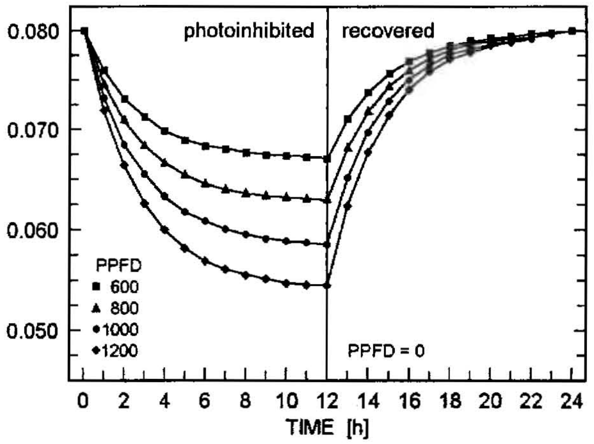

Fig. 2. Simulation of time course of photoinhibition of initial quantum yield (α) under different PPFDs (the former 12 h) and its recovery in dark condition (the later 12 h).

Physiological responses of plant to diurnal variances of environmental factors: P_N and E change in response to diurnal variations of environmental factors, in which solar radiation and temperature are the main influencing factors. Solar radiation is symmetrical with respect to the peak at noon, whereas the peak of temperature lags behind by about 2 h. Courses of the two variables determine the type of diurnal changes of P_N. Midday depression of P_N occurs due to stomatal closure at high T_l that causes high VPD and non-stomatal inhibition, such as photoinhibition (Xu and Shen 1997).

Fig. 3 shows the diurnal variations of solar radiation and air temperature that are typical at mid-latitudes. T_a increases with solar radiation after sunrise, until afternoon it will decrease when solar radiation decreases to a certain extent. The air vapour pressure was held constant, and VPD increased with T_l exponentially. We used the method of changing one environmental factor at a time to observe its influence on physiological processes while others were held constant.

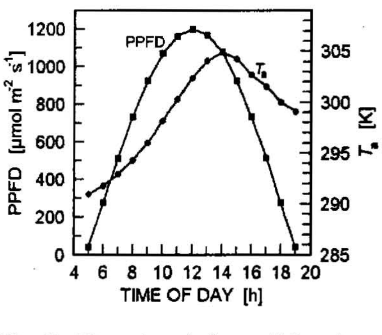

Fig. 3. Diurnal variations of the photon flux densities (PPFD) and air temperature (T_a) used in the simulation.

VPD: Water vapour pressure rather than relative humidity is preferred to represent air humidity. In this simulation, e_a was constant over the day. Different e_a values give different VPD values under the same temperatures. P_N is low and the midday depression is aggravated, when VPD is high (the figure showing the physiological effects of different VPD conditions is omitted). P_N values did not differ much under different VPD in the morning when irradiance was not high. Thus g_s decreased significantly with an increase in VPD. Generally, E increases with VPD in daytime, but above a certain value it no longer shows any increase with VPD in the afternoon, due to stomatal closure.

The fundamental difference between photoinhibited and non-photoinhibited photosynthesis is a difference in α, which is held constant (0.08) in non-photoinhibited plants. In this simulation, α responded mainly to PPFD and T_l for photoinhibited plants, so the diurnal courses of decrease in α were nearly the same under different humidity. The value of α decreased slowly in the morning, and then rapidly in the period of high irradiances, reaching its minimum around 14:00, and then increased when the recovery rate exceeded the rate of intensification of photoinhibition. A similar daily course of F_v/F_m has frequently been observed under natural conditions (Demmig-Adams *et al.* 1989). As there is a linear relation between photon yield and F_v/F_m, the simulation is in accordance with experimental results. The values of g_s and C_i/C_s also become lower under photoinhibition-inducing conditions and around noon E decreases because of stomatal closure (Morison 1987). T_l is higher under photoinhibition-inducing conditions because of a diminished rate of latent heat dissipation.

Air temperature: Temperature affects photosynthesis in two ways: the first effect is on the intrinsic speed of biochemical processes of photosynthesis, the other one is on VPD_s through its effect on the intercellular saturated vapour pressure. According to the chain of effects discussed in the preceding paragraphs, P_N decreases with increasing VPD, because of stomatal closure. It was analysed above that C_i/C_s is determined mainly by the changes in g_{sc} caused by changes in VPD, so the increase in temperature causes a monotonous decrease in C_i.

When T_a is not high (in Fig. 4, T_{max} = 28 °C), P_N shows no depression at midday, but does not increase either with the increase in PPFD because carboxylation is near its saturation. Under high T_a, as on days with temperature maximum reaching 32 °C in Fig. 4, midday depression occurs. When T_a is very high, with a daily maximum of 38 °C, the midday depression is very pronounced. The diurnal changes in g_s are similar to those of P_N in that both change widely. The decrease in E at midday is slight, because the lowering of g_s is compensated by the increase in VPD (Fig. 4). When temperature is low (T_{max} = 28 °C), E changes with its maximal value occurring at the same time as those of T_a and VPD. At higher temperatures, with T_{max} = 32 °C, its maximal value occurs near 12:00, and becomes lower when VPD reaches the peak at about 14:00. When T_a is much higher, *e.g.*, when T_{max} = 38 °C, E lowers in afternoon, though to a lesser extent than g_s, owing to the increase in VPD with the increase in T_l.

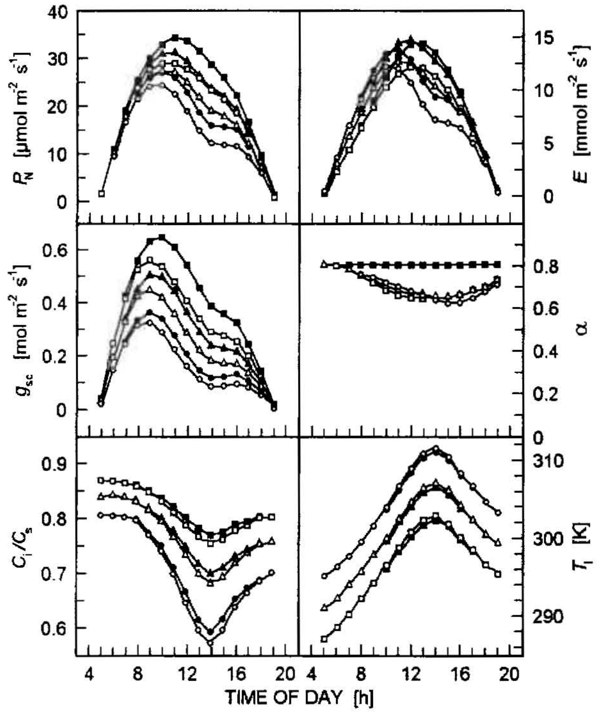

Fig. 4. The influence of air temperature (T_a) on the diurnal variances of net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance for CO$_2$ (g_{sc}). Ambient vapour pressure of 1 000 Pa, daily maximal solar radiation of 900 µmol m^{-2} s^{-1}, and 28 (*square*), 32 (*triangle*), 36 (*circle*) °C. *Open symbols* represent photoinhibition, and *full symbols* non-photoinhibition. α is held constant under non-photoinhibition condition, and changes in α are calculated by Eq. 6 under photoinhibition condition.

Under photoinhibition condition, the time courses of α change with irradiance, being different under different temperatures. P_N is lower because of photoinhibition, the difference being very large in the afternoon when α is at its minimum. Changes in E are similar with those in P_N.

T_l under condition of photoinhibition is higher than that under non-photoinhibition, the maximal differences are in the maximum temperature, when solar radiation is high and g_s is small. C_i/C_s shows its dependence on VPD between mesophyll and ambient air, so it decreases to its minimum over the day at the maximum T_l.

Solar radiation: Since solar radiation is the driving force of both photosynthesis and leaf heat balance, it influences physiological processes through photosynthesis and T_l. If T_a is far lower than the optimum and photoinhibition does not occur, the higher the solar irradiance and T_l, the higher the P_N (Fig. 5). Around noon on clear days, solar radiation always exceeds the saturation irradiance, and therefore its increase does not promote P_N noticeably. If T_a reaches or exceeds its optimal value, the increase in solar radiation, and the corresponding increases in T_l and VPD will lead to a decrease in P_N. Under higher solar irradiance accompanied by high temperature in the afternoon, P_N is low (Fig. 5). Diurnal courses of g_s are similar to those of P_N, but their midday depressions are larger and deeper. C_i/C_s decreases in midday, and shows much greater decrease under higher solar radiation (Fig. 5*E*), which is induced by higher T_l (Fig. 5*F*). So the

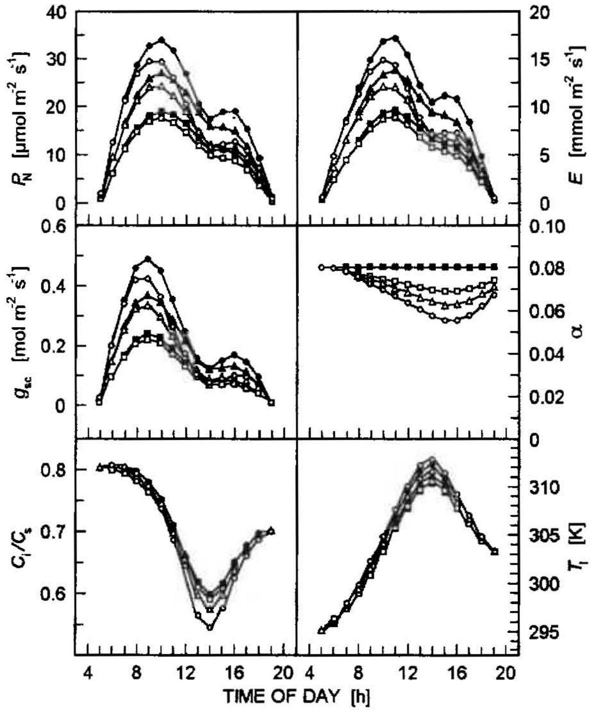

Fig. 5. The influence of solar radiation on the diurnal variances of net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance for CO$_2$ (g_{sc}). Ambient vapour pressure of 1 000 Pa, daily maximal temperature of 36 °C, and PPFDs 600 (*square*), 900 (*triangle*), and 1 200 (*circle*) µmol m^{-2} s^{-1} separately. *Open and full symbols* represent photoinhibition and non-photoinhibition, respectively.

decrease in C_i/C_s in midday shows that stomatal closure is one of the reasons causing midday depression of P_N (Farquhar and Sharkey 1982).

High solar radiation causes large decreases in α, and its recovery is slightly quicker after high solar irradiation, and has a trend to reach the same value (Fig. 5*D*). P_N, E, and g_s behave differently under photoinhibition or non-photoinhibition conditions under high irradiance. T_l under photoinhibition is higher than that under non-photoinhibition conditions, which is evident under high solar radiation around noon.

Discussion

In this paper, a method to calculate P_N under photoinhibition condition is presented. Although environmental factors are interacting outside the plant community under consideration, the change in one factor will influence another. In nature, there are still different compositions of these factors, and this method is useful in analysis of effect of various factors and is clear in concept. As the model is a general one for plant, the value of parameters may differ between species, such as shade plants and sun plants that have different characteristics in responding to irradiance (Powles 1984). The decrease in initial quantum yield starts at the primary stage of photoinhibition. A decrease in convexity of the photosynthetic irradiance-response curve and maximum carboxylation rate occurs at a deep photoinhibition (Leverenz *et al.* 1990). Falk *et al.* (1992) also found a progressive lowering of quantum yield and the rate of bending (convexity) of the irradiance response curve. It is easy to include these factors in the photoinhibition model when mathematical descriptions of the elements involved are provided. After the mechanism of photoinhibition is better understood, a model will eventually be constructed for the objective of studying biochemical processes of photoinhibition, such as degradation of D1 protein and xanthophyll cycle.

Besides the state of photosynthetic system, α is also affected by temperature and CO_2 concentration (Cannell and Thornley 1998). In our model the relation of α with some environmental factors is not included for the purpose of distinguishing photosynthesis under photoinhibition and non-photoinhibition. In the study of effects of global change on carbon cycling in ecosystems, the temperature and CO_2 elements influencing α can be easily merged.

P_N is calculated by a hyperbola, *i.e.*, irradiance response curve, which gives a gradual increase of P_N with irradiance. P_{max} will not be reached under limited irradiance, therefore, a lowering of α will bring about a lowering in calculated P_N, which will lower g_s and E according to the model. In fact, under high PPFD, P_N is mainly determined by carboxylation rate, and is weakly influenced by low efficiency of electron transport. Here only one aspect of photoinhibition is considered, *i.e.*, the decrease in α at the first stage of photoinhibition. Nevertheless, the decrease in P_{max} will cause a further lowering of P_N at a deeply inhibited stage.

The P_N and g_s model used here is basically similar to previous studies (Collatz *et al.* 1991, Leuning 1995) with a revision in g_s model by replacing P_N with P_G. This revision is based on theoretical analysis according to response curves of both P_G and g_s to irradiances. As g_s given by the revised model goes to infinity when CO_2 concentration tends to the CO_2 compensation concentration, the form of

$$g_s = \mathrm{m}A_g/[C_s(1 + \mathrm{VPD}_s/\mathrm{VPD}_a)] + g_0$$

may give a reasonable interpretation of the relations. These revisions need to be verified by critical experiments. In the BWB model, relative humidity is an atmospheric element and an input of model whereas VPD_s is an unknown variable. Therefore it is necessary to introduce an Aphalo and Jarvis (1993) model based on gaseous transfer of transpiration to make the equations complete. So the model is combined as a P_N-E-g_s model (Yu and Wang 1998).

There is considerable evidence that stomata tend to close with increasing VPD_s in most plant species (Grantz 1990, Aphalo and Jarvis 1991). Maroco *et al.* (1997) reported that in some drought-resistant species g_s showed a negative response to increasing VPD_s, whereas in drought-escaping species g_s was independent of VPD_s. Besides many relations between g_s and atmospheric humidity or VPD_s, Monteith (1995), basing on many experimental results, proposed that stomata respond to humidity in such a way that g_s decreases linearly with an increase in E. This expression is equivalent to the responses of g_s to VPD_s (Eq. 1b). It has been verified that to use VPD_s instead of relative humidity in the BWB model may markedly promote the applicability of stomatal models under natural conditions (Yu *et al.* 2000).

References

Aphalo, P.J., Jarvis, P.G.: Do stomata respond to relative humidity? – Plant Cell Environ. **14**: 127-132, 1991.

Aphalo, P.J., Jarvis, P.G.: The boundary layer and the apparent responses of stomatal conductance to wind speed and to the mole fraction of CO_2 and water vapour in the air. – Plant Cell Environ. **16**: 771-783, 1993.

Ball, J.T., Woodrow, I.E., Berry, J.A.: A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. – In: Biggins, J. (ed.): Progress in Photosynthesis Research. Vol. 4. Pp. 221-224. Nijhoff Publ., Dordrecht – Boston – Lancaster 1987.

Barták, M., Raschi, A., Tognetti, R.: Photosynthetic characteristics of sun and shade leaves in the canopy of *Arbutus unedo* L. trees exposed to *in situ* long-term elevated CO_2. – Photosynthetica **37**: 1-16, 1999.

Caemmerer, S. von, Farquhar, G.D.: Some relationship between the biochemistry of photosynthesis and the gas exchange of leaves. – Planta **153**: 376-387, 1981.

Cannell, M.G.R., Thornley, J.H.M.: Temperature and CO_2 responses of leaf and canopy photosynthesis: A clarification using the non-rectangular hyperbola model of photosynthesis. – Ann. Bot. **82**: 883-892, 1998.

Collatz, G.J., Ball, J.T., Grivet, C., Berry, J.A.: Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. – Agr. Forest Meteorol. **54**: 107-136, 1991.

Demmig, B., Björkman, O.: Comparison of the effect of excessive light on chlorophyll fluorescence (77 K) and photon yield of O_2 evolution in leaves of higher plants. – Planta **171**: 171-184, 1987.

Demmig-Adams, B., Adams, W.W., III: Photoprotection and other responses of plants to high light stress. – Annu. Rev. Plant Physiol. Plant mol Biol. **43**: 599-626, 1992.

Demmig-Adams, B., Adams, W.W., III, Winter, K., Meyer, A., Schreiber, U., Pereira, J.S., Krüger, A., Czygan, F.-C., Lange, O.L.: Photochemical efficiency of photosystem II, photon yield of O_2 evolution, photosynthetic capacity, and carotenoid composition during the midday depression of net CO_2 uptake in *Arbutus unedo* growing in Portugal. – Planta **177**: 377-387, 1989.

Edwards, G.E., Baker, N.R.: Can CO_2 assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? – Photosynth. Res. **37**: 89-102, 1993.

Falk, S., Leverenz, J.W., Samuelsson, G., Öquist, G.: Changes in Photosystem II fluorescence in *Chlamydomonas reinhardtii* exposed to increasing levels of irradiance in relationship to the photosynthetic response to light. – Photosynth. Res. **31**: 31-40, 1992.

Farquhar, G.D., Caemmerer, S. von, Berry, J.A.: A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. – Planta **149**: 78-90, 1980.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. – Annu. Rev. Plant Physiol. **33**: 317-345, 1982.

Fu, W., Wang, T.-D.: [Effects of boundary layer conductance on leaf gas exchange.] – Acta bot. sin. **36**: 614-621, 1994. [In Chin.]

Goudriaan, J., van Laar, H.H.: Relations between leaf resistance, CO_2-concentration and CO_2 assimilation in maize, beans, lalang grass and sunflower. – Photosynthetica **12**: 241-249, 1978.

Goudriaan, J., van Laar, H.H., van Keulen, H., Louwerse, W.: Photosynthesis, CO_2 and plant production. – In: Day, W., Atkin, R.K. (ed.): Wheat Growth and Modeling. Pp. 107-122. Plenum Press, New York 1985.

Grantz, D.A.: Plant response to atmospheric humidity. – Plant Cell Environ. **13**: 667-679, 1990.

Grantz, D.A., Zeiger, E.: Stomatal responses to light and leaf-air vapor pressure difference show similar kinetics in sugarcane and soybean. – Plant Physiol. **81**: 865-868, 1986.

Greer, D.H., Berry, J.A., Björkman, O.: Photoinhibition of photosynthesis in intact bean leaves: role of light and temperature, and requirement for chloroplast-protein synthesis during recovery. – Planta **168**: 253-260, 1986.

Greer, D.H., Laing, W.A.: Photoinhibition of photosynthesis in intact kiwifruit (*Actinidia deliciosa*) leaves: Recovery and its dependence on temperature. – Planta **174**: 159-165, 1988.

Hall, A.E.: A model of leaf photosynthesis and respiration for predicting carbon dioxide assimilation in different environments. – Oecologia **143**: 299-316, 1979.

Harley, P.C., Tenhunen, J.D.: Modeling for photosynthetic response of C_3 leaves to environmental factors. – In: Boote, K.J., Loomis, R.S. (ed.): Modeling Crop Photosynthesis – from Biochemistry to Canopy. Pp. 17-39. Crop Science Society of America, American Society of Agronomy, Madison 1991.

Harley, P.C., Thomas, R.B., Reynolds, J.F., Strain, B.R.: Modelling photosynthesis of cotton grown in elevated CO_2. – Plant Cell Environ. **15**: 271-282, 1992.

Jarvis, P.G.: Stomatal response to water stress in conifers. – In: Turner, N.C., Kramer, P.J. (ed.): Adaptation of Plants to Water and High Temperature Stress. Pp. 105-122. Wiley-Interscience, New York – Chichester – Brisbane – Toronto 1980.

Jarvis, P.G.: Scaling processes and problems. – Plant Cell Environ. **18**: 1079-1089, 1995.

Johnson, I.R., Thornley, J.H.M.: A model of instantaneous and daily canopy photosynthesis. – J. theor. Biol. **107**: 531-545, 1984.

Kao, W.-Y., Forseth, I.N.: Diurnal leaf movement, chlorophyll fluorescence and carbon assimilation in soybean grown under different nitrogen and water availabilities. – Plant Cell Environ. **15**: 703-710, 1992.

Leuning, R.: Modeling stomatal behaviour and photosynthesis of *Eucalyptus grandis*. – Aust. J. Plant Physiol. **17**: 159-175, 1990.

Leuning, R.: A critical appraisal of a combined stomatal photosynthesis model for C_3 plants. – Plant Cell Environ. **18**: 339-355, 1995.

Leverenz, J.W., Falk, S., Pilström, C.-M., Samuelsson, G.: The effects of photoinhibition on the photosynthetic light-response curve of green plant cells (*Chlamydomonas reinhardtii*). – Planta **182**: 161-168, 1990.

Long, S.P., Humphries, S., Falkowski, P.G.: Photoinhibition of photosynthesis in nature. – Annu. Rev. Plant Physiol. Plant mol. Biol. **45**: 633-662, 1994.

Maroco, J.P., Pereira, J.S., Chaves, M.M.: Stomatal responses to leaf-to-air vapour pressure deficit in Sahelian species. – Aust. J. Plant Physiol. **24**: 381-387, 1997.

Monteith, J.L.: Principles of Environmental Physics. – Pp. 121-124. Arnold, London 1973.

Monteith, J.L.: A reinterpretation of stomatal responses to humidity. – Plant Cell Environ. **18**: 357-364, 1995.

Morison, J.I.L.: Intercellular CO_2 concentration and stomatal response to CO_2. – In: Zeiger, E., Farquhar, G.D., Cowan, I.R. (ed.): Stomatal Function. Pp. 229-251. Stanford University Press, Stanford 1987.

Mott, K.A., Parkhurst, D.F.: Stomatal responses to humidity in air and helox. – Plant Cell Environ. **14**: 509-515, 1991.

Muraoka, H., Tang, Y., Terashima, I., Koizumi, H., Washitani, I.: Contributions of diffusional limitation, photoinhibition and photorespiration to midday depression of photosynthesis in *Arisaema heterophyllum* in the natural high light. – Plant Cell Environ. **23**: 235-250, 2000.

Ögren, E.: Prediction of photoinhibition of photosynthesis from measurements of fluorescence quenching components. – Planta **184**: 538-544, 1991.

Ögren, E., Sjöström, M.: Estimation of the effect of photoinhibition on the carbon gain in leaves of a willow canopy. – Planta **181**: 560-567, 1990.

Ottander, C., Öquist, G.: Recovery of photosynthesis in winter stressed Scots pine. – Plant Cell Environ. **14**: 345-349, 1991.

Paw U, K.T.: Mathematical analysis of the operative temperature and energy budget. – J. therm. Biol. **12**: 227-233, 1987.

Powles, S.B.: Photoinhibition of photosynthesis induced by visible light. – Annu. Rev. Plant Physiol. **35**: 15-44, 1984.

Powles, S.B., Björkman, O.: Photoinhibition of photosynthesis: effect on chlorophyll fluorescence at 77 K in intact leaves and in chloroplast membranes of *Nerium oleander*. – Planta **156**: 97-107, 1982.

Schuepp, P.H.: Transley review No.59: Leaf boundary layers. – New Phytol. **125**: 477- 507, 1993.

Sheriff, D.W.: Epidermal transpiration and stomatal responses to humidity: some hypotheses explored. – Plant Cell Environ. **7**: 669-677, 1984.

Tyystjärvi, E., Mäenpää, P., Aro, E.-M.: Mathematical modelling of photoinhibition and Photosystem II repair cycle. I. Photoinhibition and D1 protein degradation *in vitro* and in the absence of chloroplast protein synthesis *in vivo*. – Photosynth. Res. **41**: 439-449, 1994.

Wong, S.C., Cowan, I.R., Farquhar, G.D.: Stomatal conductance correlates with photosynthetic capacity. – Nature **282**: 424-426, 1979.

Wong, S.-C., Cowan, I.R., Farquhar, G.D.: Leaf conductance in relation to rate of CO_2 assimilation. I. Influence of nitrogen nutrition, phosphorus nutrition, photon flux density, and ambient partial pressure of CO_2 during ontogeny. – Plant Physiol. **78**: 821- 825, 1985a.

Wong, S.-C., Cowan, I.R., Farquhar, G.D.: Leaf conductance in relation to rate of CO_2 assimilation. II. Effects of short-term exposures to different photon flux densities. – Plant Physiol. **78**: 826-829, 1985b.

Wong, S.-C., Cowan, I.R., Farquhar, G.D.: Leaf conductance in relation to rate of CO_2 assimilation. III. Influences of water stress and photoinhibition. – Plant Physiol. **78**: 830-834, 1985c.

Xu, D.-Q., Shen, Y.-K.: Midday depression of photosynthesis. – In: Pessarakli, M. (ed.): Handbook of Photosynthesis. Pp. 451-459. Marcel Dekker, New York – Basel – Hong Kong 1997.

Yu, Q., Liu, J.D., Luo, Y.: Applicability of some stomatal models to natural conditions. – Acta bot. sin. **42**: 203-206, 2000.

Yu, Q., Wang, T.D.: Simulation of the physiological responses of C_3 plant leaves to environmental factors by a model which combines stomatal conductance, photosynthesis and transpiration. – Acta bot. sin. **40**: 740-754, 1998.