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AN ANALYTICAL MODEL FOR GAS EXCHANGE STUDIES OF PHOTOSYNTHESIS

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Abstract

A steady-state model designed especially for analysis of gas exchange studies of terrestrial net photosynthesis is discussed. The model expresses net photosynthesis as a function of light, temperature, CO_2 concentration, stomatal resistance, and other factors. The parameters of the model are estimated from data by nonlinear least-squares. The data set must consist of simultaneous observations of net photosynthesis, light energy, leaf temperature, and leaf resistance. The model accounted for 89% of the variance in the data set and gave good predictions of photosynthesis. This model can be used for data analysis and as a process model for simulation.

Introduction

The advent of the infrared gas analyzer system stimulated a great deal of research in photosynthesis of terrestrial plants. Much effort has gone into the development of methodology (see Sestak, Catsky and Jarvis 1971) but mathematical analysis of the results of the studies for the most part has been somewhat limited. A great deal has been learned about the photosynthetic response of plants to various factors, but the researcher would usually vary only one factor while assuming that the rest of the important factors were constant or nonlimiting (Walker et al. 1972). Field studies of photosynthesis (e.g., Helms 1972), have been limited primarily to measurement of photosynthesis and environmental factors and attempts to explain the observations from a more or less qualitative point of view. Using this approach, researchers were forced to speculate as to whether an observed midday depression of photosynthetic uptake was caused by stomatal closure, high temperatures, or a combination of both factors. A working, realistic mathematical model can greatly aid researchers in data analysis and experimental design.

Reed and Webb (1972) have emphasized that a photosynthesis model must account for the effects of at least the major factors in order to explain the behavior of the complex series of processes involved in photosynthesis. Most of the models reported in the literature either do not account for all the known physical variables affecting photosynthesis or they have a number of parameters that can be neither measured nor estimated, thus rendering them inadequate for general use. For example, Chartier (1969, 1970) developed a model of photosynthesis as a function of light and CO_2 concentration, but his model was directed primarily toward investigation of various internal resistances to CO_2 flux, and neglected the effects of temperature on photosynthetic rates. Lommen et al. (1971) developed a model describing the behavior of photosynthesis with respect to CO_2 concentration, radiant energy, and temperature, but were unable to incorporate leaf respiration into their model without including unmeasurable parameters. They were therefore limited to using a simplified version of their model, which neglected respiration and failed to completely characterize temperature effects on photosynthesis. Taylor and Sexton (1972) incorporated a temperature function in the simplified model of Lommen et al. for simulation of photosynthesis.

The model described herein was developed to reflect the physical nature of the system while remaining sufficiently simple to be useful. In this model, photosynthesis is described as a function of four principal factors: light, temperature, CO_2 concentration, and stomatal resistance. The model is modular, so that when a subsequent improvement of a subsystem function is developed it can be inserted into the overall model without changing its essential structure. All parameters of the model can be estimated from experimental data either graphically or by nonlinear least-squares; the physical variables must be measured, if not, a realistic mathematical model must be used to provide the necessary input.

Derivation of the Model

Gaastra (1959) derived a steady-state expression for net photosynthesis from Fick's first law of diffusion:

$$P_n = \frac{C_o - C_i}{R} \tag{1}$$

where P_n = net photosynthesis, C_o = external CO_2 concentration, C_i = internal CO_2 concentration, and R = resistance to CO_2 flux. Lommen et al. (1971) solved equation (1) for C_i and substituted it into a Michaelis-Menten expression of photosynthesis as a function of C_i, obtaining a quadratic equation solved for P_n, where C_i was defined as CO_2 concentration at the site of fixation.

We defined C_i as the concentration of CO_2 in the substomatal cavity because Gaastra's solution (equation 1) of Fick's first law holds only when the flux rate is independent of path length (Crank 1970); letting C_i = chloroplast CO_2 concentration may violate the assumption that flux is independent of path length and necessitates the use of a series of resistances that cannot be measured. We modeled C_i as a function of three fluxes of CO_2: the flux through the stomata, the flux from the substomatal cavity into the mesophyll (photosynthesis P), and the flux from the cells into the substomatal cavity (Respiration W) (Figure 1). Net stomatal CO_2 flux can be in either direction, depending on the relative magnitude of the photosynthetic and respiratory rates. The substomatal CO_2 concentration C_i is a state variable, the units of which are mass per unit volume. We chose mg liter^{-1}, which is equivalent to mg dm^{-3}, because it is convenient to express photosynthetic rates as mg dm^{-2}hr^{-1}.

The steady-state flux through the stomata can be defined by Fick's first law, $F = D\partial C/\partial z$, which can be solved to give

$$F = \frac{-D(C_i - C_o)}{z_2 - z_1} = \frac{-D\Delta C}{\Delta z} \tag{2}$$

Gaastra (1959) defined the resistance to CO_2 flux, R as $\Delta z/D$, giving equation (1). The variable D is diffusivity of CO_2 in air, commonly in units of $cm^2 \ sec^{-1}$, and is actually a complicated function including a laminar diffusivity component, and diffusivity as affected by stomatal pore shape and size (Jarvis 1971). If we multiply equation (2) by R, given Gaastra's definition of R, D and Δz are cancelled leaving only ΔC (g dm^{-3}). We have, in a sense, multiplied a flux by an inverse velocity, giving the concentration of material in the path at a given instant. We did not, however, wish to define R in terms of diffusivity and distance, instead preferring the option of defining R in terms of stomatal aperture and density, boundary layer resistance, water potential, and so on. Nevertheless, the effect of multiplying equation (2) by R is the same; the units cancel leaving a density with units of mass per unit volume. The resulting equation is:

$$F' = \frac{-RD' \ \Delta C}{\Delta z} \ (\text{mg dm}^{-3}) \tag{3}$$

where F' is CO_2 density in stomatal diffusion path and D' = laminar diffusivity of CO_2 in air. The other components of D will be cancelled by their corresponding values in the measured quantity R.

Likewise, multiplication of the photosynthetic and respiratory fluxes P and W by their respective internal resistances gives the densities of CO_2 in the other two paths at any instant. Thus we can express steady-state substomatal CO_2 concentration as

$$C_i = RF + r_w W - r_p P \ (\text{mg dm}^{-3}) \tag{4}$$

where R is stomatal and boundary layer resistance (hr dm^{-1}), and r_w and r_p are internal resistances to respiration and photosynthesis, respectively. We assume that C_i is uniform throughout the substomatal cavity.

The terms $r_p P$ and $r_w W$ represent the densities of CO_2 in the photosynthetic and respiratory paths which are very difficult to measure. We can rewrite equation (4) to give:

$$C_i = RF + r_d W_d - r_{pw} P_i \tag{5}$$

where W_d is dark respiration (mitochondrial) and P_i is internal net photosynthesis, $P_i = P - W_p$, where W_p is photorespiration (perioxysomal) with units mg $dm^{-2}hr^{-1}$.

Substituting equation (3) into equation (5) we have:

$$C_i = \frac{RDC_o}{\Delta z} - \frac{RDC_i}{\Delta z} + r_d W_d - r_{pw} P_i \tag{6}$$

Letting $r_w W_d = W_d'$ and $r_{pw} P_i = P_i'$ and solving equation (6) for C_i, we have:

$$C_i = \frac{RDC_o + \quad z(W_d' - P_i')}{RD + \Delta z} \tag{7}$$

where P_i' and W_d' are densities with units mg dm^{-3}. Equation (7) could be substituted into equation (1) if W_d' and P_i' were known, but this is not the case; these quantities must be modeled as described below.

We used a Michaelis-Menten relation to define net photosynthesis as a function of light (Lommen et al. 1971, Horn 1971).

$$P_i(L) = \frac{\omega L}{L + K_L}, \tag{8}$$

where ω is the maximum value of photosynthesis and $K_L = L$ when $P_i(L) = \omega/2$ (Lommen et al. 1971). The parameter   is a function of temperature T, as is K_L. For simplicity we, like Lommen et al., assumed that $dK_L/dT = 0$. Our estimates of K_L represent the mean value of K_L over an entire range of temperature. Unlike Lommen et al., we let $\omega = g(T)$.

From data on photosynthetic rates as affected by temperature (e.g., Pisek and Winkler [1958], Webb [1972], and our own data) we observe that the temperature dependence on photosynthesis is a more or less symmetrical quadratic, which can be described by equation (9):

$$g(T) = \kappa T(\alpha - T)^{\beta} \tag{9}$$

where α is the high-temperature intercept of the curve, κ is related to the area under the curve, and β gives the skew. Equation (9) is substituted into equation (8), which is then substituted into another Michaelis-Menten relationship, again from Lommen et al. (1971), giving P_i as a function of light, temperature, and CO_2 concentration:

$$P_i = \frac{\{[\kappa T(\alpha - T)^{\beta}]\ L(L + K_L)^{-1}\}C_i}{C_i + K} \tag{10}$$

where C_i = substomatal CO_2 concentration and K is the Michaelis-Menten constant of CO_2-dependent reactions. Equation (10) gives a family of curves similar to those shown in Lommen et al. It is important to remember that P_i is internal *net* photosynthetic flux. Equation (10) is multiplied by r_{pw} to obtain P_i', the CO_2 density in the diffusion path.

The internal resistance values in this model cannot be directly estimated by nonlinear least-squares because the value of κ is strongly correlated with r_{pw}; as r_{pw} increases, κ decreases. Thus we estimate a new parameter κ', which equals $r_{pw}\kappa$. This presents no problem if r_w is relatively constant. Otherwise, r_{pw} would have to be modeled as a function of whatever factors affect it. We assumed that r_{pw} is constant, thus equation (10) becomes

$$P_i' = \frac{\{[\kappa' T(\alpha - T)^{\beta}]L(L + K_L)^{-1}\}C_i}{C_i + K} = \frac{P_i'(T,L)C_i}{C_i + K} \text{ (mg dm}^{-3}\text{)} \tag{11}$$

Dark respiration rate can be defined as an exponential function of temperature: $W_d = \gamma \exp(\delta T)$. Internal resistance to dark respiration r_d can also be subsumed into γ, giving γ'. If mitochondrial respiration W_d is inhibited by light (Jackson and Volk 1970, Zelitch 1971), then δ will be diminished as light increases. The reduction of δ in light may be caused by a limitation of substrate or cofactors being used in perioxysomal respiration. If we assume a first-order limitation of W_d as light increases we can express δ as a first-order decay with light, $\delta = \delta_o e^{-\varepsilon L}$.

Hence, our model of CO_2 density in the dark respiration path is somewhat simplistically defined as

$$W'_d = \gamma' \exp(T\delta_o e^{-\varepsilon L}) \text{ (mg dm}^{-3}\text{)} \tag{12}$$

Having defined the terms P'_i and W'_d we then substitute them into equation (7), but it is necessary to eliminate the unknown, C_i, from P'_i in equation (11). By solving equation (7) for P'_i we have:

$$P'_i = \frac{1}{\Delta z}[RD'C_o - C_i(RD' + \Delta z)] + W'_d \tag{13}$$

Setting equationnn(11) equal to equation (13), we have:

$$\frac{P'_i(T,L)C_i}{C_i + K} = \frac{1}{\Delta z}[RD'C_o - C_i(RD' + \Delta z)] + W'_d \tag{14}$$

which can be rewritten to give

$$C_i^2(RD' + \Delta z) + C_i K(RD' + \Delta z) + \Delta z[P_i(T,L) - W'_d] - RD'C_o$$
$$+ K(-RD'C_o - zW'_d) = 0 \tag{15}$$

Equation (15) has the form $ax^2 + bx + c = 0$ and can be solved for C_i by means of the quadratic formula, the positive root of which is appropriate here. The solution of equation (15) for C_i can then be substituted into equation (1) giving a relatively complete model of net photosynthesis:

$$P_n = \frac{1}{R}\left(C_o - \frac{-b + \sqrt{b^2 - 4ac}}{2a}\right) \tag{16}$$

where $a = RD' + \Delta z$; $b = aK + \Delta z[P'_i(T,L) - W'_d] - RD'C_o$, and $C = K(-RD'C_o - \Delta z W'_d)$.

This model accounts for the known effects of light, temperature, CO_2 concentration, and stomatal resistance on photosynthesis. Further, if more resolution is desired, it is possible to replace terms or subsystem models (e.g., P'_i, W'_d, D', R, etc.) with more elaborate or rigorous models without destroying the essential structure of the model.

Experimental Methods

Experimental data for parameter estimation and validation of the model were obtained by measuring CO_2 exchanges by *in situ* specimens of mature yellow poplar (*Liriodendron tulipifera* L.) during August and September 1971. Gas analyses were carried out through use of an open-type gas exchange apparatus incorporating a Beckman IR-215A nondispersive infrared gas analyzer and several temperature-regulated polyfilm cuvettes (Dinger 1971; Dinger, Goldstein, and Mankin 1972).

Sample chambers were positioned variously within the upper canopies of test specimens in order to remove variation in photosynthetic rate attributable to shade adaptation. Flow rates through the chambers were adjusted to 12 l min^{-1}.

Leaf and air temperatures were measured with type-T copper-constantan thermocouples. Incident solar radiation levels (0.3-3.0 μm) were monitored by means of Lintronic dome-type solarimeters positioned at sample level. Stomatal resistance measurements were not taken during the above sampling interval; however results of subsequent field observations using techniques of diffusion resistance porometry reveal that leaf resistance in yellow poplar is largely light regulated (B. E. Dinger, unpublished data). Temperature and moisture stress appear to be minimal within habitats occupied by this species, consequently stomatal aperture appears to be controlled by light. Values for the light-dependence of leaf resistance were obtained from data for yellow poplar seedlings (Richardson, Dinger, and Harris 1972). These data were used to develop a model of stomatal resistance as a function of light energy, which model was substituted into equation (16).

The experimental data were punched on computer cards; each card containing an hourly measurement of ambient CO_2 concentration, light energy, leaf temperature, and the corresponding observation of net photosynthesis. These cards were separated into three sets; 279 cards were used for parameter estimation, forty-five other cards were used to evaluate the predictive capabilities of the model using parameter estimates from the first data set. The third data set consisted of 14 sequential hourly observations and was used as a final evaluation of the predictive capabilities of the model.

Parameter Estimation

The model has a number of terms that must be measured or estimated. The purely physical factors, C_O, R, D', Δz, L, and T, can be measured or modeled. The biological responses to the physical variables are characterized by the parameters κ', α, β, γ', δ, ε, K_L, and K. These parameters reflect the biological potential of the plant to respond to physical stimuli, and can be estimated simultaneously (Webb 1972).

We estimated all the parameters except by nonlinear least-squares fit of equation (16) to data set 1 using a modified version of BMDX85 program on the CDC 6400 computer at the University of Washington (see Draper and Smith 1966 for a discussion of nonlinear least-squares). Because of the paucity of high-temperature observations, it was necessary to weight the higher temperature data. The CO_2 constant K was estimated graphically because the natural range of C_O is too narrow for least-squares estimation. As stated above, stomatal resistance was calculated as a function of light. Laminar diffusivity was expressed as $D' = 4.82 + 0.032\ T$ ($\text{dm}^2\ \text{hr}^{-1}$) from data presented by Sestak, Jarvis and Catsky (1971). The length of the diffusion path through the stomatal pore, Δz, was initially estimated from photomicrographs (Harris, Witherspoon and Olson 1970). Subsequently, a least-squares estimation of $\Delta z = 71.7$ μm was used.

The model fit the data well as demonstrated by residual analysis. Figure 2 is a plot of the residuals (residual = observed P_n - predicted P_n) versus the observed P_n as given by the parameter values in Table 1. The residuals reflect the error both in the model and in the data. If the model is basically correct, then the residuals should be distributed normally about zero. The even distribution and lack of skew of the residuals in Figure 2 indicate that the model does fit the data well and that error of prediction is random. The variance is quite high largely because light energy impinging on the foliage was not measured; the solarimeters were located at the cuvette level but not inside the cuvettes. Hence, a sunfleck striking the leaves would increase photosynthesis, but the increased radiation would not be recorded, and *vice versa* light sensors inside the cuvettes would improve predictability.

Figures 3 through 5 show the output of equation (16) in terms of light, temperature, and CO_2 concentration. The curves in Figures 3-5 show that tulip poplar is adapted to high light intensity by having a rather high light saturation (shown also by the value of K_L), and has a temperature optimum of about 32°C (given by the parameter β). Analysis of the residuals with respect to C_o showed a very good fit to the data even with a "guessed" value of K, the Michaelis-Menten coefficient. Note that the model predicts light, temperature, and CO_2 compensation points. The relation of the light curve to the data points is shown in Figure 6 and the effect of leaf resistance on P_n is illustrated in Figure 7. The relation in Figure 7 is equivalent to $f(R) = 1/aR^2$ where a is a constant. This relation is supported by Richardson Dinger and Harris (1972) who displayed a plot of observed P_n versus $1/r_s$ that deviated from linearity. This relation will be discussed in greater detail in a subsequent section.

The three-dimensional surface in Figure 8 shows the shape of the response surface of equation (16) with respect to light and temperature. Note that the model predicts extremely high respiration rates as temperature increases. Examination of Figure 2 shows a good fit to the respiration data (where P_n is negative), but the curve in Figure 8 is unreasonable. This points out a principal data requirement of nonlinear least-squares parameter estimation: the observed data must vary over a reasonable range of the independent variables. We modeled respiration as a function of temperature and light, but the range of temperature over which we had observations was 19° to 25°C. This range is much too narrow for nonlinear least-squares parameter estimation. It is also likely that the respiration function used (equation 12) is inadequate. Certainly additional studies of factors affecting respiration at the leaf level are indicated.

The flow rates we used introduced substantial CO_2 depletions (35-90 ppm) inside the chambers, resulting in somewhat lower net photosynthesis than would be expected. This problem has since been rectified with the Chamber CO_2 concentrations being held to within ±10% of ambient CO_2 levels. Subsequent studies show net photosynthesis rates on the order of 8 to 13 mg dm^{-2} hr^{-1} for various hardwood species, including yellow poplar. At this writing, however, the CO_2-limited data suffice to demonstrate the applicability of nonlinear least-squares parameter estimation.

Our results show that it is possible to obtain reasonable fits even when the data are not ideally distributed over the variable space. However the ideal procedure would be to vary the climate inside the cuvettes to obtain observations of P_n at high light and low temperatures, low light and high temperatures, and so on. These data would then give an unbiased estimate of the parameters. Further, it is imperative to simultaneously measure all the independent variables because they affect photosynthesis in concert.

Model Validation and Sensitivity to Parameters

Having estimated parameters from one data set, and using these parameter values, we compared the model's output against the second data set consisting of 45 observations of L, T, C_o, and P_n taken at a different time. The model's predictions agreed well with observed P_n. The residuals again were normally distributed about zero with an R^2 of 0.775 indicating that the model accounted for 77.5% of the variance in the validation set (as opposed to $R^2 = 0.89$ for the parameter estimation run). A parameter estimation run on this data set gave no improvement in the fit of the model to the data.

A second test of the predictive power of the model consisted of comparing the model's prediction to observed P_n on 19 August 1971 (Figure 9) (data set 3). The model was quite sensitive to light and gave a good approximation of the diurnal photosynthesis curve. The model tended to overpredict, illustrating the effect of CO_2 drawdown in the chambers. Had the CO_2 concentration inside the chambers been used for C_o, the prediction would have improved. Even though the input data were not wholly adequate, Figure 9 shows that the model and the parameter estimates are sufficiently accurate to allow the model to be used as a predictive tool.

The model is quite sensitive to some of the parameters and variables (Table 2). It is interesting and counter-intuitive that the photosynthetic rate P_n increases with an increase of diffusion path length Δz while P_n decreases with an increase in laminar diffusivity D when all other factors are constant. This behavior can be understood by remembering that we defined the substomatal CO_2 concentration C_i as the sum of the CO_2 densities in the three diffusion paths. The flux through the stomates is given by equation (1), and the CO density in the stomatal path by equation (3). Dividing equation (1) by equation (3) and solving for P_n cancels ΔC giving

$$P_n = \frac{\Delta z}{D'R} F' \text{ (mg dm}^{-2}\text{ hr}^{-1}) \qquad (17)$$

Equation (17) explains the relation of CO_2 flux through the stomata P_n, to the stomatal path CO_2 density F', and accounts for the observations in Table 2 and Figure 7, when the other variables are held constant. In nature, R is strongly related to Δz and D' and one would not vary without affecting the others. Thus, although equation (17) predicts an increase in P_n with an increase in Δz, in nature R would increase with Δz and because of the dominance of R, the net result would be a reduction in P_n. Likewise, an increase in D' would result in a decrease in R, effectively increasing P_n. Equation (17) demonstrates the importance of measuring these variables. Because D' is temperature dependent, and Δz may vary from sun to shade leaves and from species to species, error in these values will result in some error of prediction. Systematic error in the estimates of Δz and D' are compensated by other parameters, principally κ', but if Δz varies greatly from plant to plant, poor measurement will result in a systematic error in prediction. Likewise, because of the temperature dependence of D', it is desirable to measure leaf resistance R concurrently with P_n in order to compensate for the error in our model of D' as a function of temperature. We were not able to do this, but our model of R as a function of light was sufficiently accurate to give good predictions of P_n because of the dominance of R in equation (17).

The effect of the two Michaelis-Menten coefficients K, and K_L on P_n is as expected because as K and K_L increase the slope of the Michaelis-Menten functions decrease resulting in a lower P_n at a given value of light or CO_2 concentration. The parameter κ' is related to the area under the curve given by equation (11) with respect to temperature; as κ' increases so does P_n.

In conclusion, we believe that the model given by equation (16) is a valid steady-state description of the photosynthetic process at the level observed by gas exchange studies. The model behaves well and is a good predictor. Further, the fact that we use a least-squares parameter estimation procedure allows the model to be used analytically much as a linear regression model (Draper and Smith 1966). The use of the model for data naalysis and comparison of photosynthetic rates of various species under varying natural conditions in the topic of a paper now in preparation.

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Table 1. Estimated values of the parameter set from 279 observations, weighted nonlinear least-squares.

$\kappa' = 0.15435$

$\alpha = 44.0$

$\beta = 0.34979$

$K_L = 0.32725$

$K = 0.275$*

$\gamma' = 0.78192$

$\delta = 0.21532$

$\varepsilon = 437.62$

*K estimated graphically

Table 2. Sensitivity of model (equation 16) to changes in values of some parameters and variables at constant light (1.2 cal cm^{-2} min^{-1}), temperature (29°C) ambient CO_2 concentration (.583 mg ℓ^{-1}) and stomatal resistance (4 sec cm^{-1}). The column headed corrected change is percent change in P_n with a 10% change in the parameter.

Parameter	Value	% Change	P_n	% Change	Corrected % Change
Δz	60	——	4.346	——	——
(μm)	70	14.3	5.040	13.8	9.6
	80	12.5	5.725	12.0	9.6
D	4.0	——	7.271	——	——
(hr dm^{-2})	5.0	20.0	5.891	19.0	9.5
	6.0	17.0	4.950	16.0	9.4
K	0.3	——	5.019	——	——
	0.4	25.0	4.547	9.4	3.8
	0.5	20.0	4.166	8.4	4.2
K_L	0.3	——	5.226	——	——
	0.4	25.0	4.939	5.5	2.2
	0.5	20.0	4.684	5.2	2.6
κ'	0.08	——	4.992	——	——
	0.10	20.0	6.076	17.8	8.9
	0.15	33.3	8.707	30.2	9.0

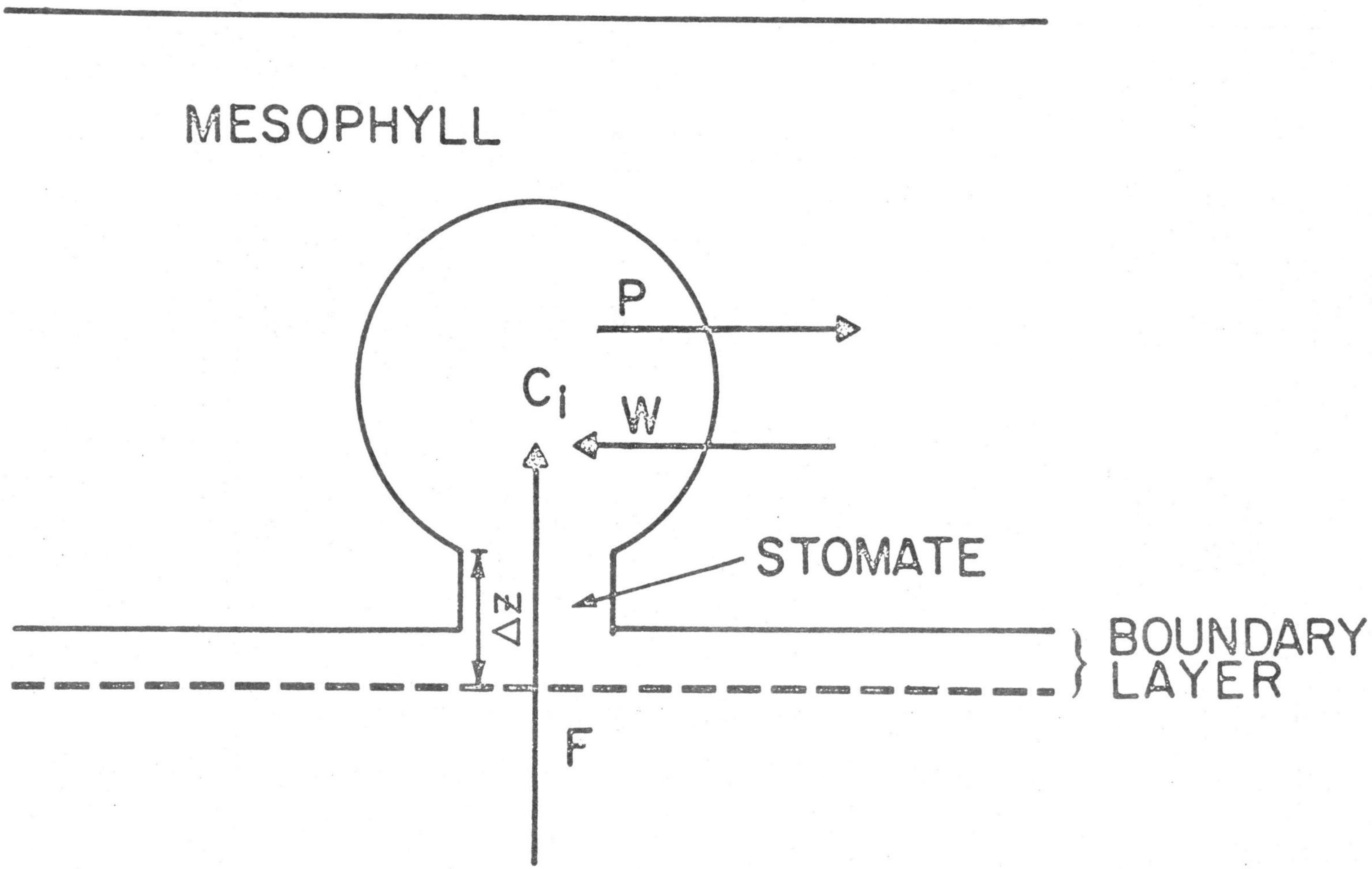

Figure 1. Diagram of leaf cross-section through a stomate showing the CO_2 diffusion paths considered by the model (description of symbols in text).

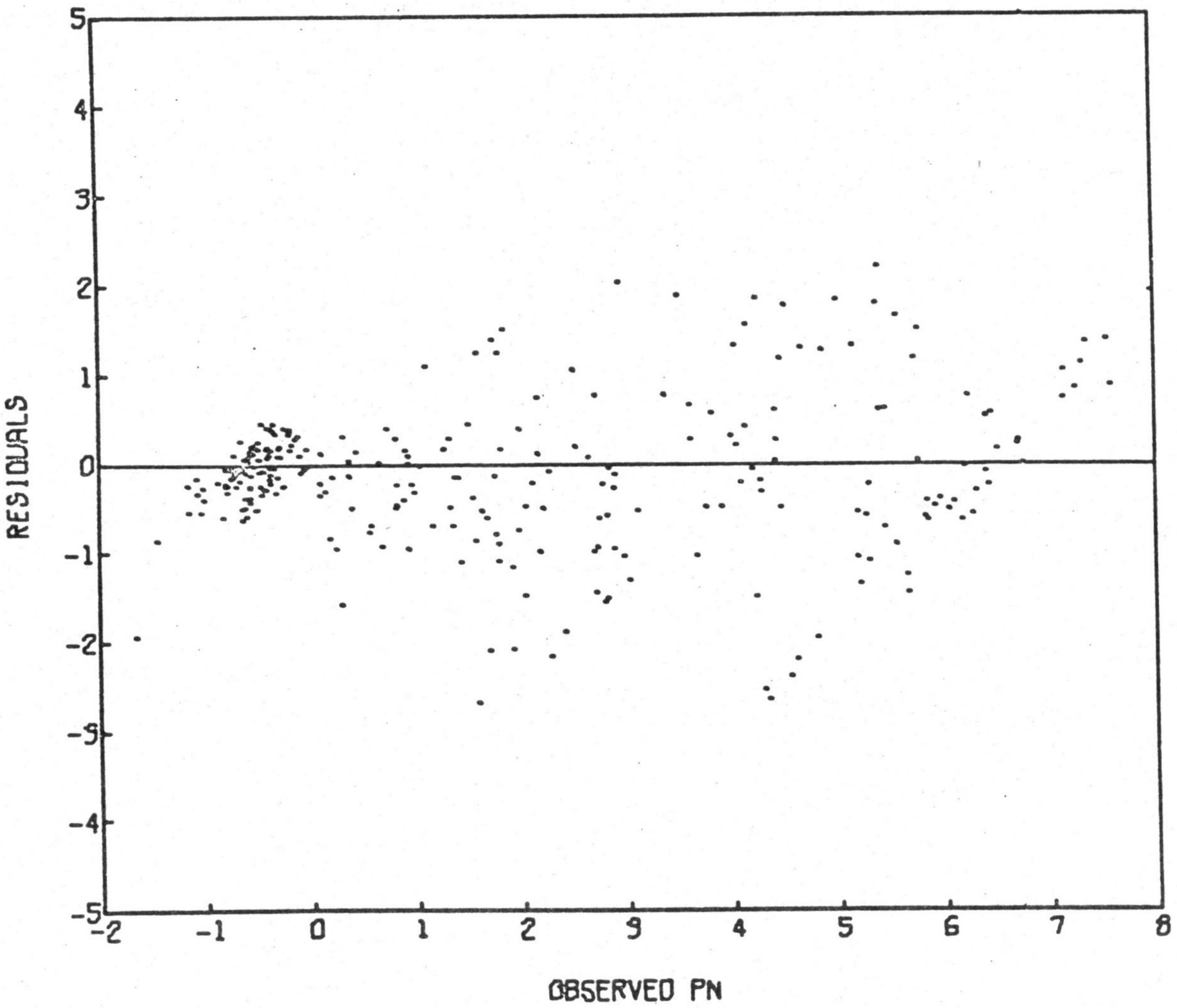

Figure 2. The distribution of residuals (observed P_n - predicted P_n) as related to observed P_n. Data set 1.

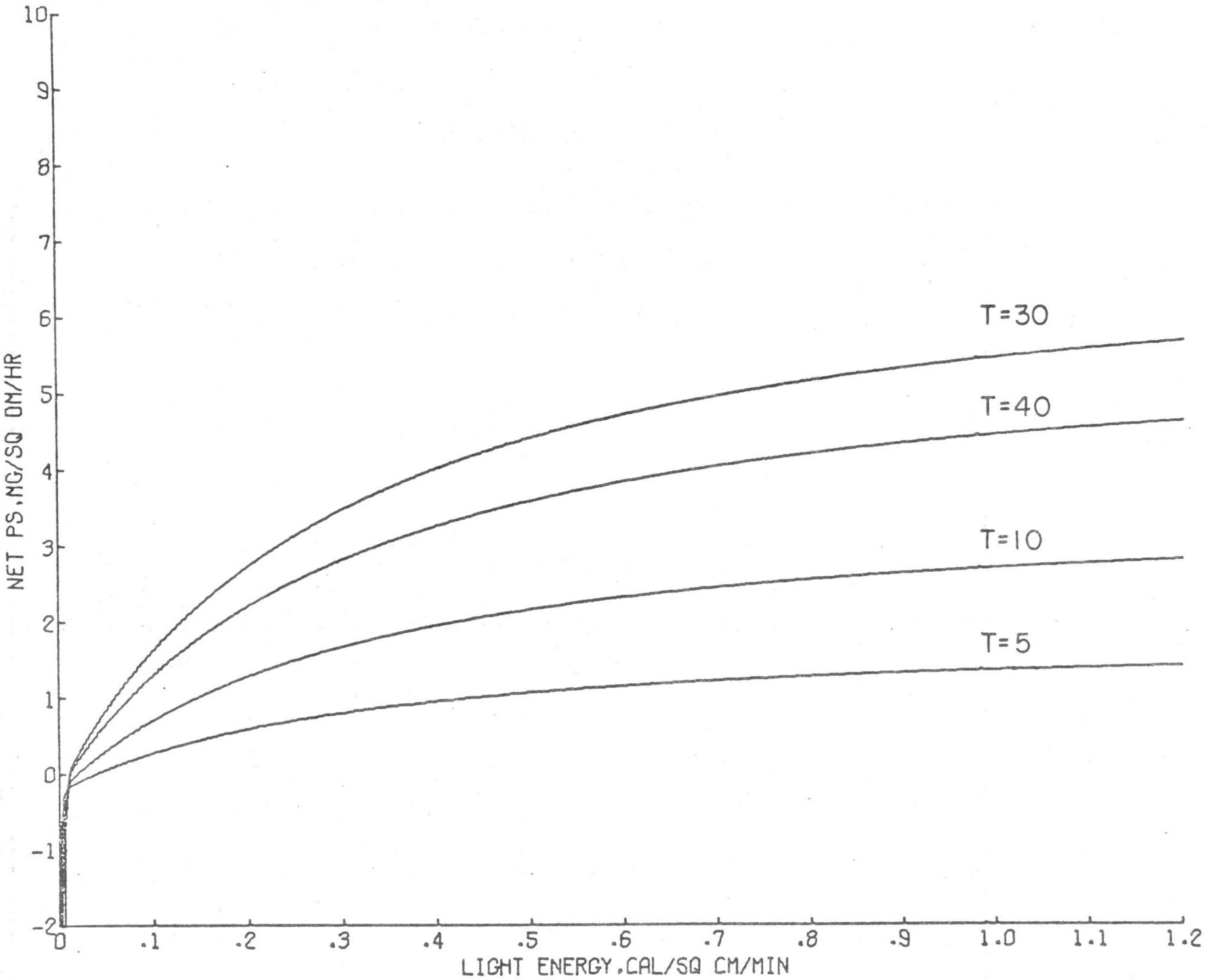

Figure 3. Predicted net photosynthesis as related to radiant energy at 4 temperatures (°C), C_O = 0.583 mg ℓ^{-1}.

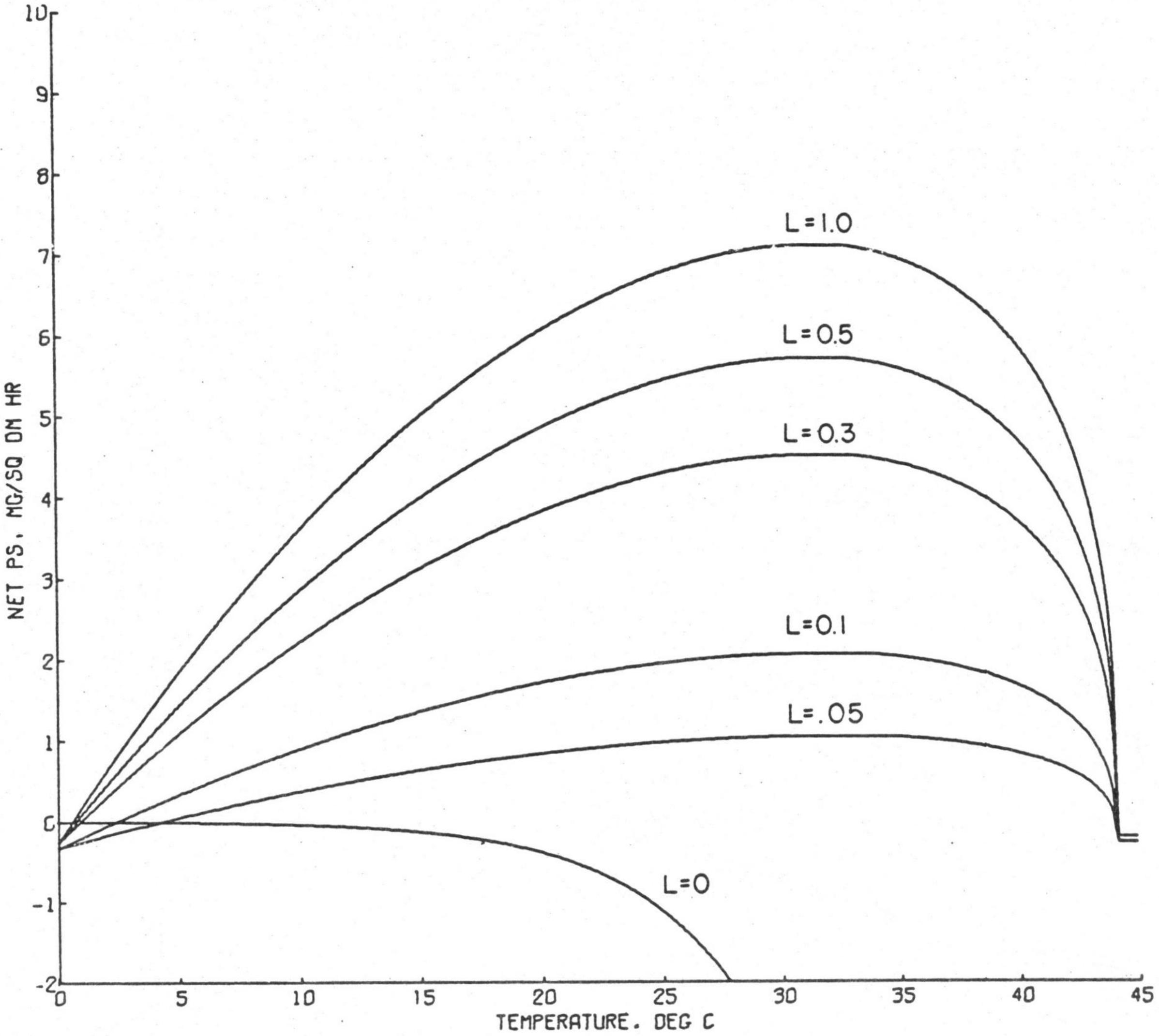

Figure 4. Predicted net photosynthesis as related to temperature at 4 radiant energy levels (cal cm^{-2} min^{-1}), R = 4 sec cm^{-1}, C_o = 0.583 mg ℓ^{-1}.

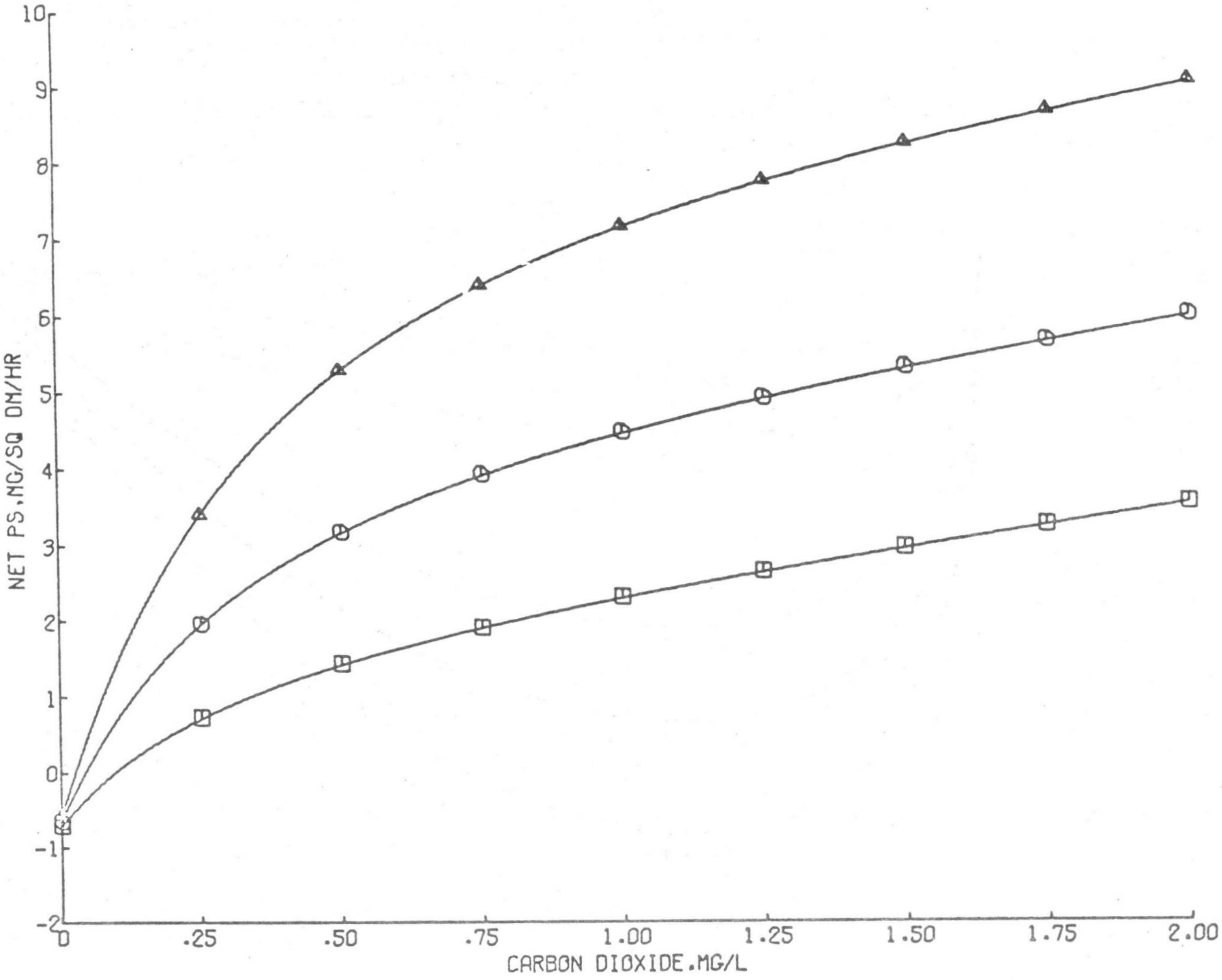

Figure 5. Predicted net photosynthesis as related to ambient CO_2 concentration at 3 light intensities, *box*: L = 0.1; *circle*: L = 0.3; *triangle*: L = 1.2 cal cm^{-2} min^{-1}, T = 25°C, R = 4 sec cm^{-1}.

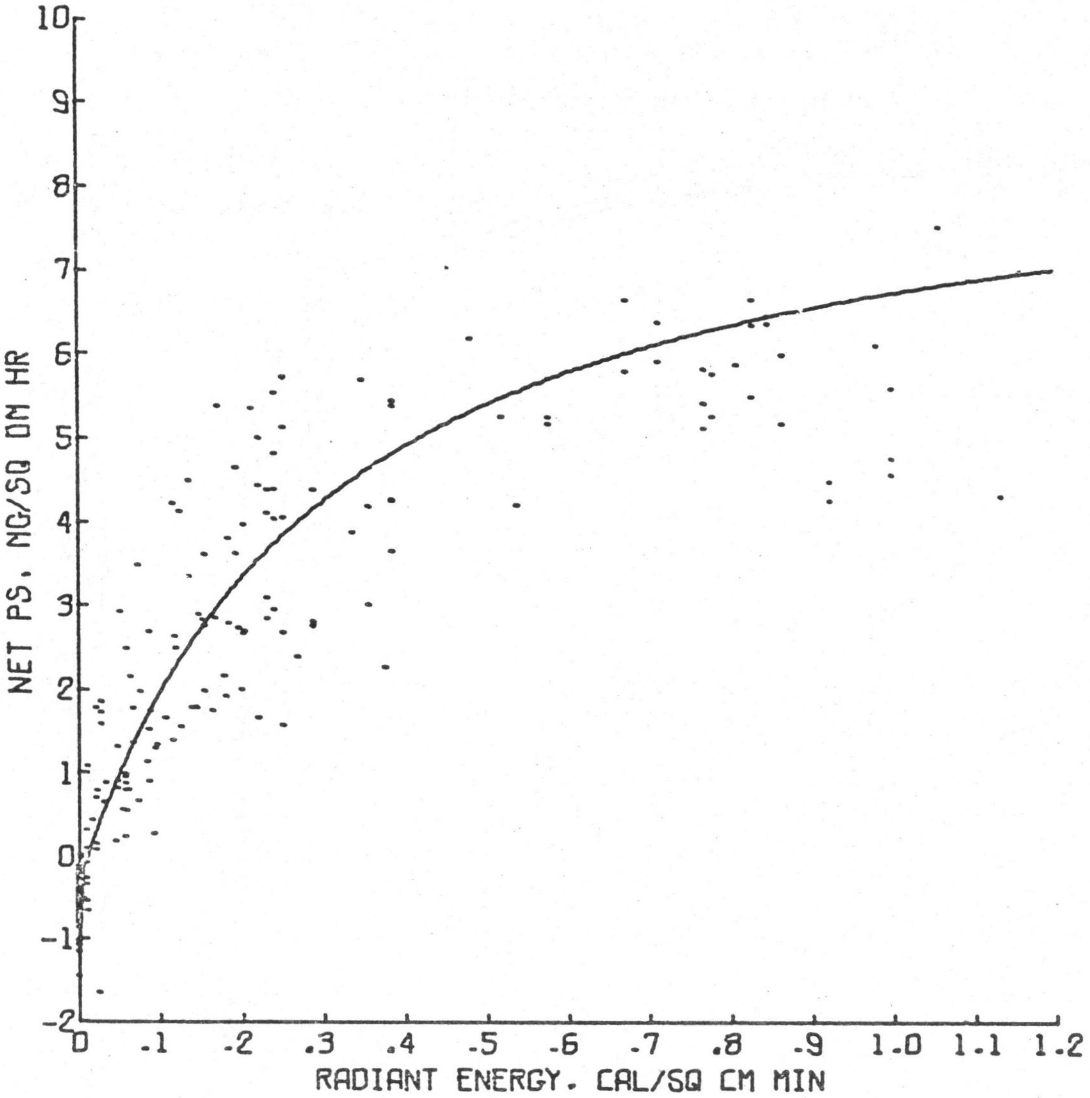

Figure 6. Predicted P_n at 25°C, $C_o = 0.583$, (smooth curve) compared to data points of data set 1 which range between 20 and 30°C.

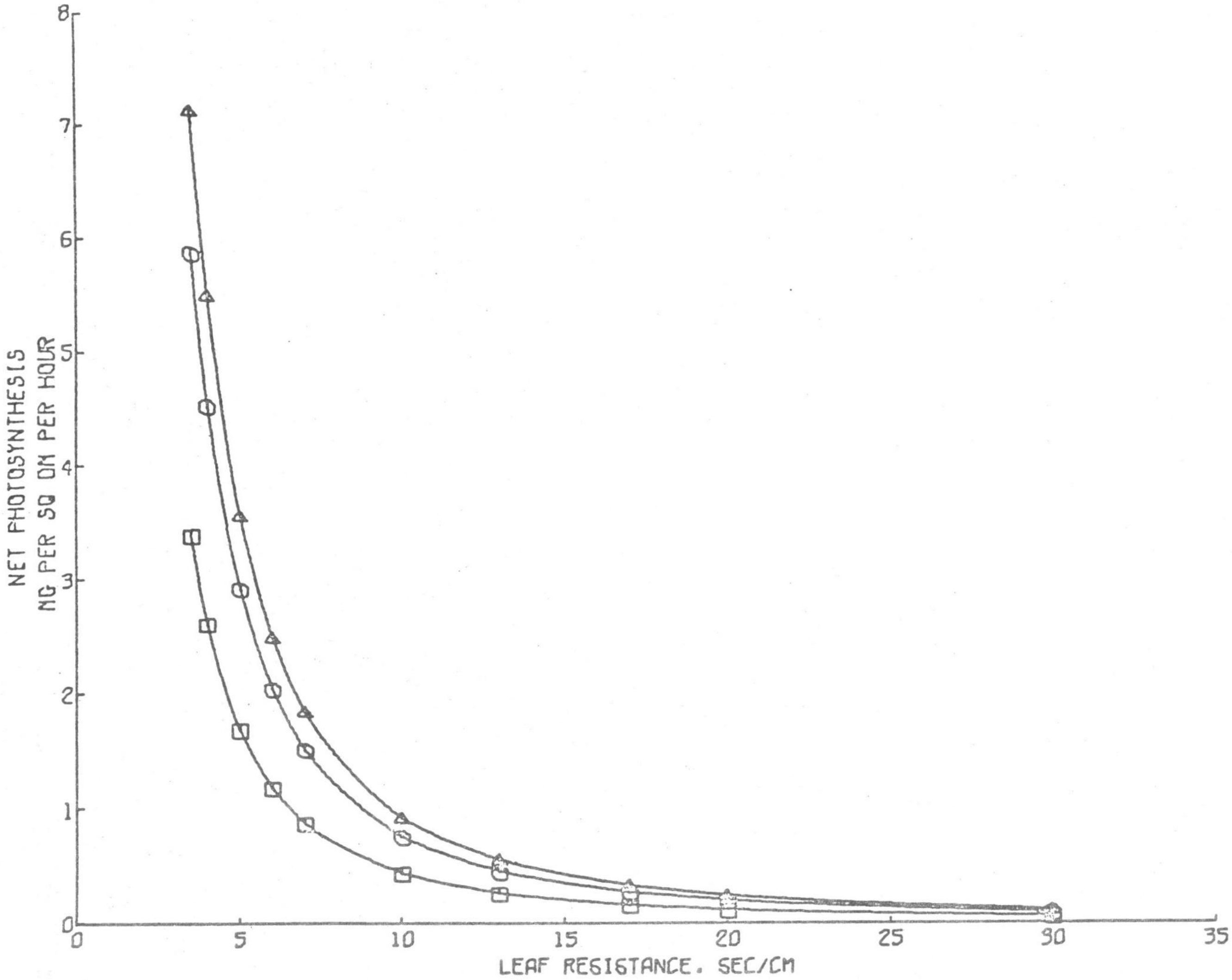

Figure 7. Predicted P_n as related to leaf resistance at T = 25°C, C_o = 0.583 mg ℓ^{-1}, *box*: L = 0.2; *circle*: L = 0.6; *triangle*: L = 1.2 cal cm^{-2} min^{-1}.

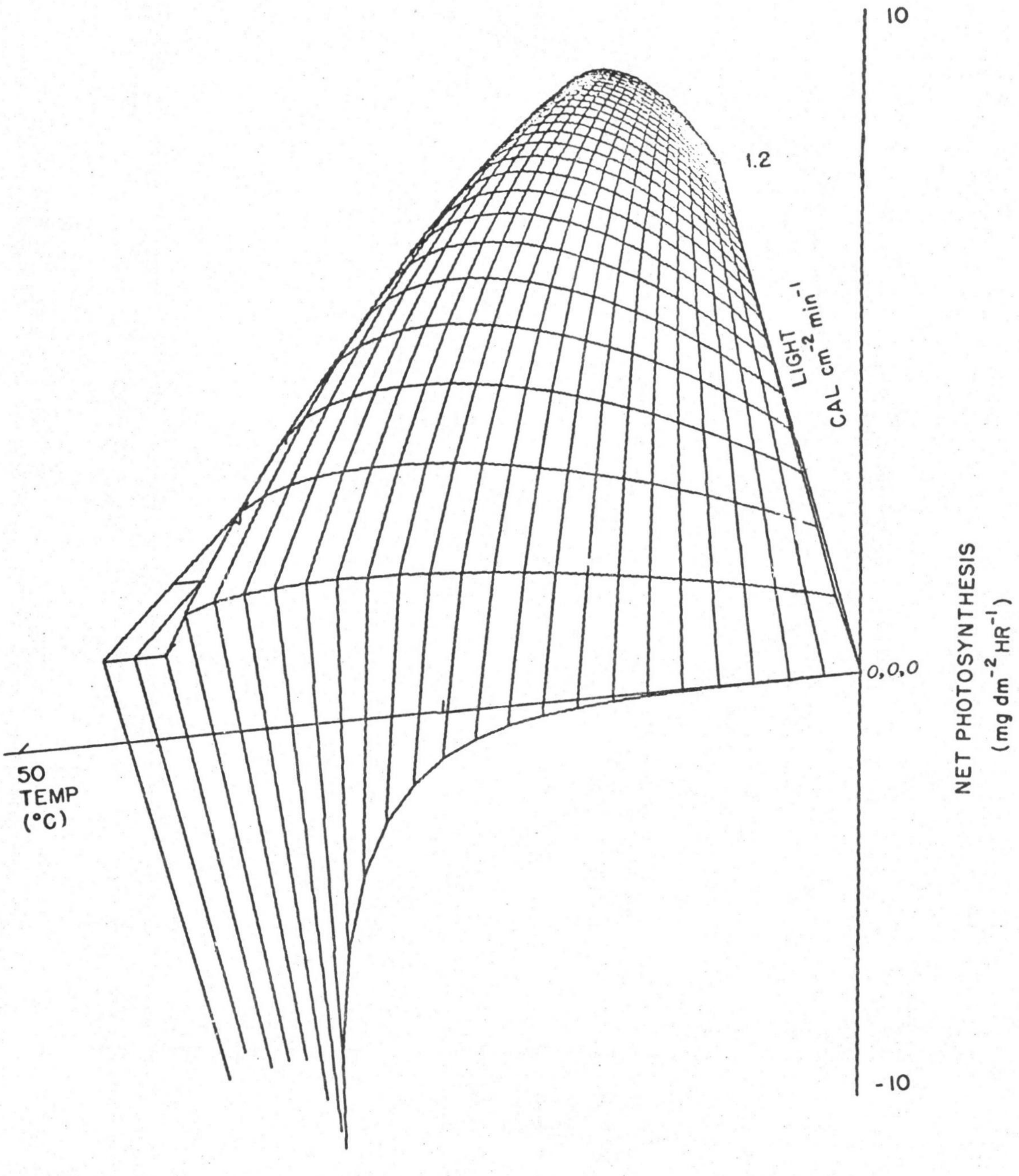

Figure 8. Three-dimensional view of light-temperature response surface of the model. $R = 4$ sec cm^{-1}, $C_o = 0.583$ mg ℓ^{-1}.

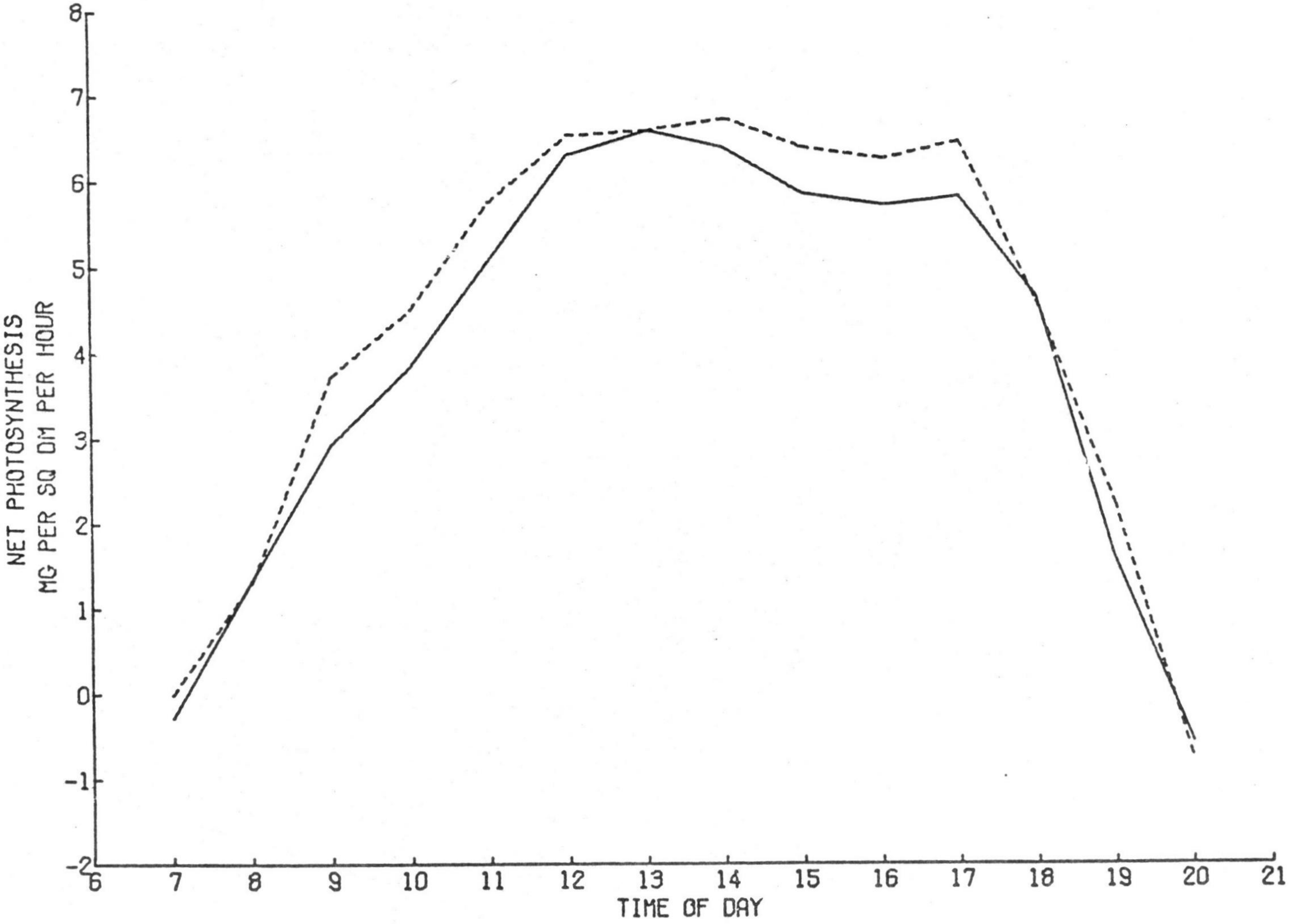

Figure 9. Comparison of predicted (dashed line) to observed net photosynthesis (solid line) of 19 August 1971. Observed environmental variables used for model input.