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COTTON CANOPY PHOTOSYNTHESIS MODEL FOR PREDICTING THE EFFECT OF TEMPERATURE AND ELEVATED CARBON DIOXIDE CONCENTRATION

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PACHEPSKY L. B., REDDY V. R. and ACOCK B. *Cotton canopy photosynthesis model for predicting the effect of temperature and elevated carbon dioxide concentration.* BIOTRONICS 23, 35-46, 1994. A four-step process for building a cotton canopy photosynthesis model is proposed. Experimental data were obtained from measurements of canopy CO₂ exchange of cotton grown in daylit controlled-environment chambers in a range of CO₂ concentrations ([CO₂]) and temperatures. The first step in modeling was to fit the hyperbolic model of canopy photosynthesis to light response curves for each combination of temperature and [CO₂]. The second step included selecting equations that describe the dependencies of the parameters of the hyperbolic model on temperature and [CO₂]. The third step was to combine these equations with the hyperbolic model in a composite model. Then the parameters in the equations were recalculated fitting the composite model to the entire data set. This fourth step proved to be essential for good model accuracy. The resulting composite model was shown to be qualitatively and quantitatively adequate to describe the effects of light, temperature, and [CO₂] in predicting cotton productivity in a changing environment.

Key words: *Gossypium hirsutum* L.; cotton; photosynthesis; step-by-step modeling; validation; parameterization.

INTRODUCTION

Carbon dioxide concentration ([CO₂]) in the atmosphere is increasing and is expected to change the global climate, leading to an increase in air temperature (25). The responses of plants to elevated [CO₂] and temperature have become important subjects of research. These responses depend on species and they are complicated by interactions between various factors (9). Numerous publications have documented the marked response of cotton to an increase in [CO₂]. In a survey of more than 400 studies, Kimball (16) calculated that doubling [CO₂] produces an average 33% increase in crop yield, with cotton showing a much stronger response.

Models are valuable tools to predict the growth and yield of crops in conditions of increasing atmospheric $[\text{CO}_2]$ and temperature (4). Crop photosynthesis models represent a necessary component of the models used to estimate crop productivity in a changing environment. The dependence of crop photosynthesis on light intensity has a characteristic hyperbolic shape. It is often expressed by Acock's (1) equation:

$$P = \frac{\alpha_c I \tau_c C}{\alpha_c I + \tau_c C} + \beta \quad (1)$$

where P is gross canopy CO_2 exchange rate, $\text{mg m}^{-2} \text{s}^{-1}$; I is the light flux density incident on the canopy, W m^{-2} ; C is $[\text{CO}_2]$ in air, mg m^{-3} ; α_c is canopy light utilization efficiency, $\text{mg CO}_2 \text{ W}^{-1}$; τ_c is canopy conductance to CO_2 transfer, m s^{-1} ; and β is a matching term, $\text{mg m}^{-2} \text{s}^{-1}$, related to the net excess of respiration over photosynthesis at low light intensities.

The hyperbolic model Eq. (1) has been used in simulating the productivity of various crops (2), including cotton crops (24). However there have been no attempts to validate this model in an elevated $[\text{CO}_2]$ environment. The purpose of this research was (i) to assess and quantify the applicability of the model Eq. (1) to simulation of photosynthetic response to light intensity at elevated $[\text{CO}_2]$ and temperature, and (ii) to analyze the dependencies of model parameters α_c , τ_c , and β on environmental variables.

MATERIALS AND METHODS

Cotton (*Gossypium hirsutum* L., cv. DPL 50) seeds were selected for uniformity and planted in 11 rows with 5 plants per row in naturally irradiated controlled-environment plant growth chambers previously described (24). The chambers consisted of a steel bin containing the rooting medium and measuring 1.0 m high by 2.0 m long by 0.5 m wide. An acrylic base on top of this soil bin held the aerial parts of the plants and measured 2.0 m high by 2.0 m long by 1.5 m wide. The soil was a mixture of sand and vermiculite with slow-release micronutrients. Some plant rows were gradually removed as plants grew to reduce competition for light. Graded shade cloths were hung around the chambers' sides up to plant height to simulate the decreased light intensity caused by adjacent plants in field conditions.

Various temperatures and $[\text{CO}_2]$ were imposed at 15 days after emergence (DAE). In the first experiment, air temperatures in the growth chambers were maintained at 15/7, 20/12, 25/17, 30/22, and 35/27°C (day/night). Carbon dioxide concentrations were maintained at 350 or 700 $\mu\text{L L}^{-1}$ at every temperature level. In the second experiment $[\text{CO}_2]$ were maintained in four chambers at 450, 600, 750 and 900 $\mu\text{L L}^{-1}$, all with the same temperature (30/18°C day/night).

Air temperature, $[\text{CO}_2]$, and irrigation in the chambers were computer controlled and/or monitored. The temperatures in the growth chambers were maintained to within $\pm 0.1^\circ\text{C}$ of the set points for 95% of the time, CO_2

concentrations to within $\pm 10 \mu\text{L L}^{-1}$. Irradiance was more variable in the afternoon than in the morning. The maximal value of irradiance each day varied between 670 and $1,030 \text{ W m}^{-2}$.

Dewpoint temperatures were not controlled but were measured at 10-s intervals with gold mirror hygrometers installed inside the return air line. The variability of dewpoint temperature was higher in daytime than in nighttime but both were relatively stable during the experimental period. Hence the humidity for every treatment did not change significantly and varied around 60%. The wind speed associated with air circulation in the cabinets was constant at 6.9 Km/hr.

Each night, the leakage rate of each chamber was determined automatically (3). During the day, the amount of CO_2 injected, the air chamber volume, atmospheric pressure, chamber temperature, and chamber leakage rate were used to calculate net canopy photosynthetic or respiratory rates over each 15-min interval. Carbon dioxide injection rates were recorded manually three times per day. Photosynthetically active radiation (PAR) was integrated over the same 15 min and used to produce daily plots of net photosynthesis vs PAR.

Gross canopy CO_2 exchange rate was calculated by subtracting dark respiration rate measured at daytime temperature during the first hour of the night, from all values of measured net photosynthesis rate. These calculations were performed during flowering at 63 DAE for the various day/night temperatures and at 83-102 DAE for the various $[\text{CO}_2]$.

DATA ANALYSIS

Since the dependencies of CO_2 exchange rate on environmental factors are known to be nonlinear (1), we took the following steps in the data analysis:

Step 1. Assess the ability of Eq. (1) to fit the data on CO_2 exchange vs. light intensity for various environmental conditions.

Step 2. Find the equations that describe the dependencies of Eq. (1) parameters on temperature and $[\text{CO}_2]$ and fit these dependencies to the values obtained in Step 1.

Step 3. Insert these equations into Eq. (1) to obtain the composite model of the dependence of CO_2 exchange rate on light intensity, temperature, and $[\text{CO}_2]$.

Step 4. Fit the composite model to the entire data set.

Two types of criteria for model performance were used to accomplish Step 1. The quantitative adequacy of the model to describe the data set was assessed by comparing the variability of the observed data with the variability of the model prediction. The F-test was used to compare estimates of the lack-of-fit variance and the pure error variance. If there were no significant differences between them the model could be considered quantitatively adequate (13, 23, 26). The critical value of the F statistic was $F_{N-k, k-p}$, where N is the total number of measurements including all replications, k is the number of treatments, and p is the number of model parameters. Qualitative adequacy of the model was tested by the autocorrelation coefficient of model errors. The absence of significant

difference between the autocorrelation coefficient and zero indicated a qualitative correspondence between the model and the data (21).

To perform Step 2, we visualized the dependencies of the estimated parameters of Eq. (1) on temperature and $[\text{CO}_2]$. The required equation had to follow the shapes of the dependencies and have $N/3$ or fewer parameters. The quality of the approximation was characterized by the correlation coefficient between the values of the parameters estimated by fitting Eq. (1) and the values of the parameters calculated by the equation under consideration. We could not use any criteria based on the variability of the residuals because we had estimates of the standard errors of the coefficients but no estimates of the standard deviations of the coefficients.

When performing Step 4, we kept the functional structure of the equation found in Step 2. However, the values of the parameters in these equations were no longer considered valid. Instead, they were treated as the first approximation because, in general, a multiple nonlinear regression (the composite model) cannot be reduced to a series of nonlinear regressions of a lower order (the component equations). Therefore, even though Eq. (1) fitted well to each experimental light response curve, and the equation fitted well to the dependencies of the Eq. (1) parameters on temperature and $[\text{CO}_2]$, their combination might not have been an optimal fit to the entire data set if the parameter values in the equations had been preserved. These coefficients needed to be adjusted because of the nonlinearity of the composite model. Hence Step 4 was necessary.

A modified Marquardt algorithm was used to calculate all nonlinear regressions (20). Estimates of parameters and standard errors of estimates were calculated. A significance level $p \leq 0.01$ was accepted for all statistical tests.

RESULTS

Typical examples of the experimental data sets are presented in Fig. 1. The scatter of photosynthesis rate data in temperatures of 25/17 (Fig. 1e) and 35/27°C (Fig. 1f) was small and was approximately the same for all values of $[\text{CO}_2]$. However, for both the 350 and 700 $\mu\text{L L}^{-1}$ $[\text{CO}_2]$, at the lower temperatures of 15/7 and 20/12°C the scatter of the data was significantly larger. This was caused by a smaller signal/noise ratio.

The parameters resulting from data fitting and statistical analysis are shown in Table 1. Analysis of the quantitative adequacy of the model by F-test showed that the model adequately described the experimental data in all 14 cases ($F < F_{k-p, N-k}$, Table 1). The analysis of residuals demonstrated the qualitative adequacy of the model. The residuals were randomly distributed along the light intensity axis (Fig. 2). The hypothesis of zero median could not be rejected for all treatments. The autocorrelation coefficient values κ were lower than the critical value κ_{cr} in 11 cases, and in the other 3 cases the value of κ was close to the critical value (Table 1).

The estimated average canopy light utilization efficiency values α_c are

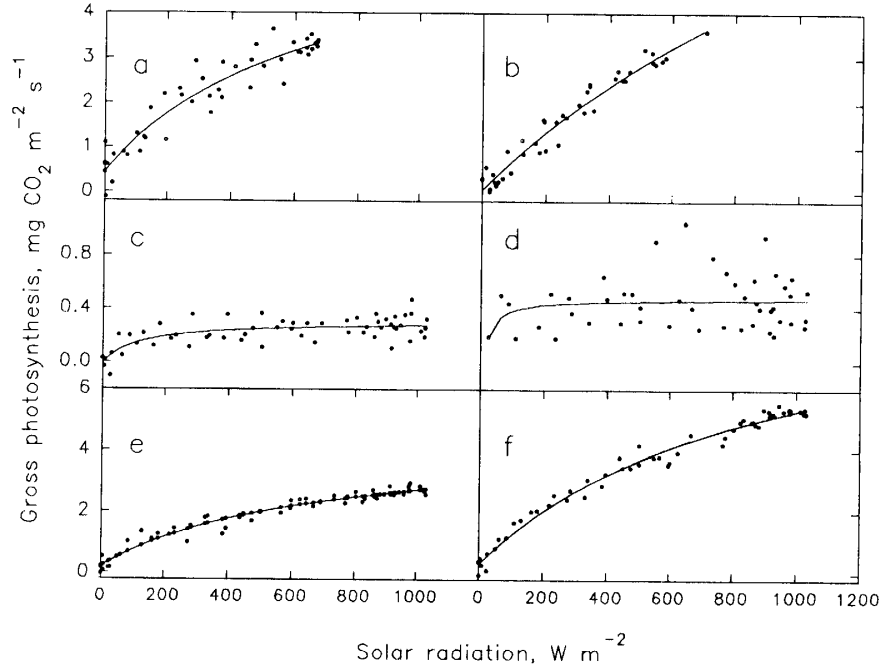


Fig. 1. Photosynthesis light response curves for a cotton canopy, measured points and fitted curves for various treatments: a-30/18°C, 450 ppm [CO₂]; b-30/18°C, 900 ppm [CO₂]; c-15/7°C, 350 ppm [CO₂]; d-20/12°C, 700 ppm [CO₂]; e-25/17°C, 350 ppm [CO₂]; f-35/27°C, 700 ppm [CO₂].

Table 1. Parameters and performance statistics of the hyperbolic model Eq. (1) calculated for various [CO₂] and day/night temperatures, T_d/T_n . Values of canopy light utilization efficiency, α_c , canopy conductance to CO₂ transfer, τ_c , and matching term, β were estimated by F statistics with critical value $F_{k-p, N-k}$ and by coefficient of autocorrelation, κ , with critical value κ_{cr} .

No	Treatment		Parameters			Statistics			
	[CO ₂], ppm	T_d/T_n , °C	$\alpha_c \times 10^3$, mg W ⁻¹	$\tau_c \times 10^3$, m s ⁻¹	β , mg m ⁻² s ⁻¹	$F_{k-p, N-k}$	F	κ_{cr}	κ
1	450	30/18	8.64	12.85	0.43	2.80	0.59	0.27	0.17
2	600	30/18	10.54	7.79	0.41	2.92	1.17	0.30	0.05
3	750	30/18	10.57	9.59	0.26	3.07	0.52	0.30	0.18
4	900	30/18	7.29	13.15	0.06	2.92	1.91	0.30	0.00
5	350	15/7	2.80	0.90	0.01	2.41	0.68	0.25	0.25
6	350	20/12	2.80	1.86	-0.05	2.41	2.22	0.25	0.05
7	350	25/17	6.15	12.07	0.19	2.41	0.91	0.25	0.14
8	350	30/22	6.66	14.72	0.49	2.54	0.89	0.25	0.25
9	350	35/27	7.90	15.52	0.46	2.54	1.79	0.25	0.26
10	700	15/7	3.09	0.47	0.13	2.50	0.83	0.25	0.19
11	700	20/12	3.23	2.31	0.19	2.50	0.79	0.25	0.16
12	700	25/17	6.65	8.45	0.12	2.54	1.56	0.25	0.02
13	700	30/22	10.61	11.82	0.45	2.54	1.13	0.25	0.17
14	700	35/27	10.57	13.64	0.30	2.54	1.36	0.25	0.15

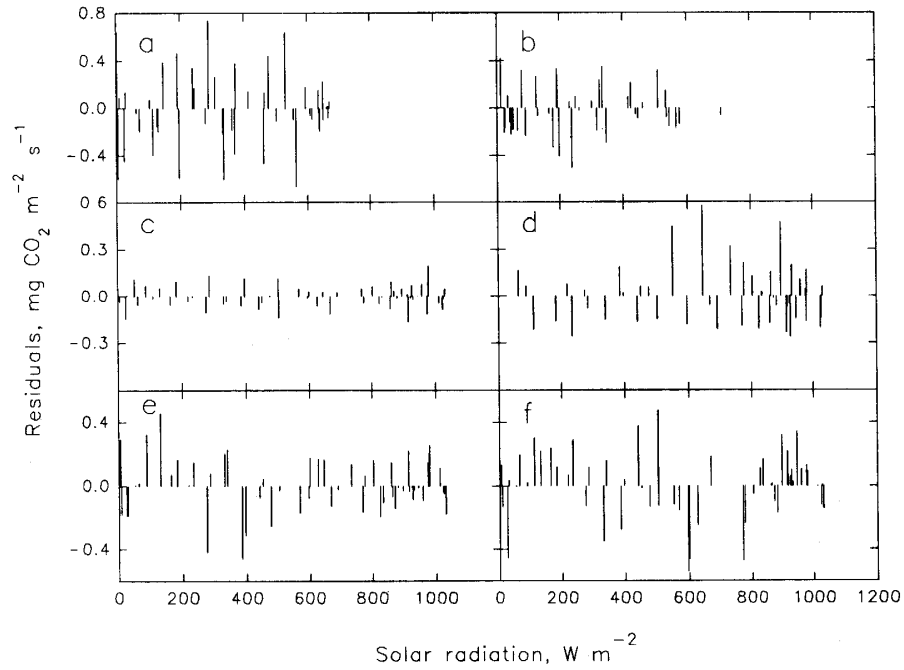


Fig. 2. Residuals for the hyperbolic model [Eq. (1)] for the same treatments as in Fig. 1, a through f.

depicted in Fig. 3a. They varied from 0.00277 to 0.01061 mg CO₂ W⁻¹ (Table 1). The estimated standard errors of α_c were rather high, as shown in Fig. 3a and there were no statistically significant differences between the estimated average α_c values corresponding to different temperatures and [CO₂]. However the distribution of estimated averages in Fig. 3a suggests that average α_c depends both on temperature and [CO₂]. We chose the logistic approximation of the dependence:

$$\frac{\alpha_{max} - \alpha_c}{\alpha_{max} - \alpha_{min}} = \frac{1}{1 + e^{\frac{T - T_{50,a}}{q_\alpha}}} \quad (2)$$

where α_{max} is the upper limit of the α_c values; α_{min} is the lower limit of the α_c values; $T_{50,a}$ is the temperature at which the curve has an inflection point and the α_c value is midway between α_{max} and α_{min} ; and q_α is a steepness factor that shows the steepness of the transition of the α_c value from α_{max} to α_{min} as the temperature increases. We assumed the upper limit α_{max} to be linearly dependent on [CO₂] so that $\alpha_{max} = \alpha_{max,amb} + b_\alpha [\text{CO}_2]$. The parameters of Eq. (2) are listed in Table 2. Calculated values of α_c are compared with estimated averages in Fig. 3. The correlation coefficient is equal to 0.91.

The estimated values of canopy conductance to CO₂ transfer τ_c are shown in Fig. 3b. They ranged from 0.47×10^{-3} to 0.016 m s⁻¹ (Table 1). The dependence of τ_c on temperature is statistically significant and has the same

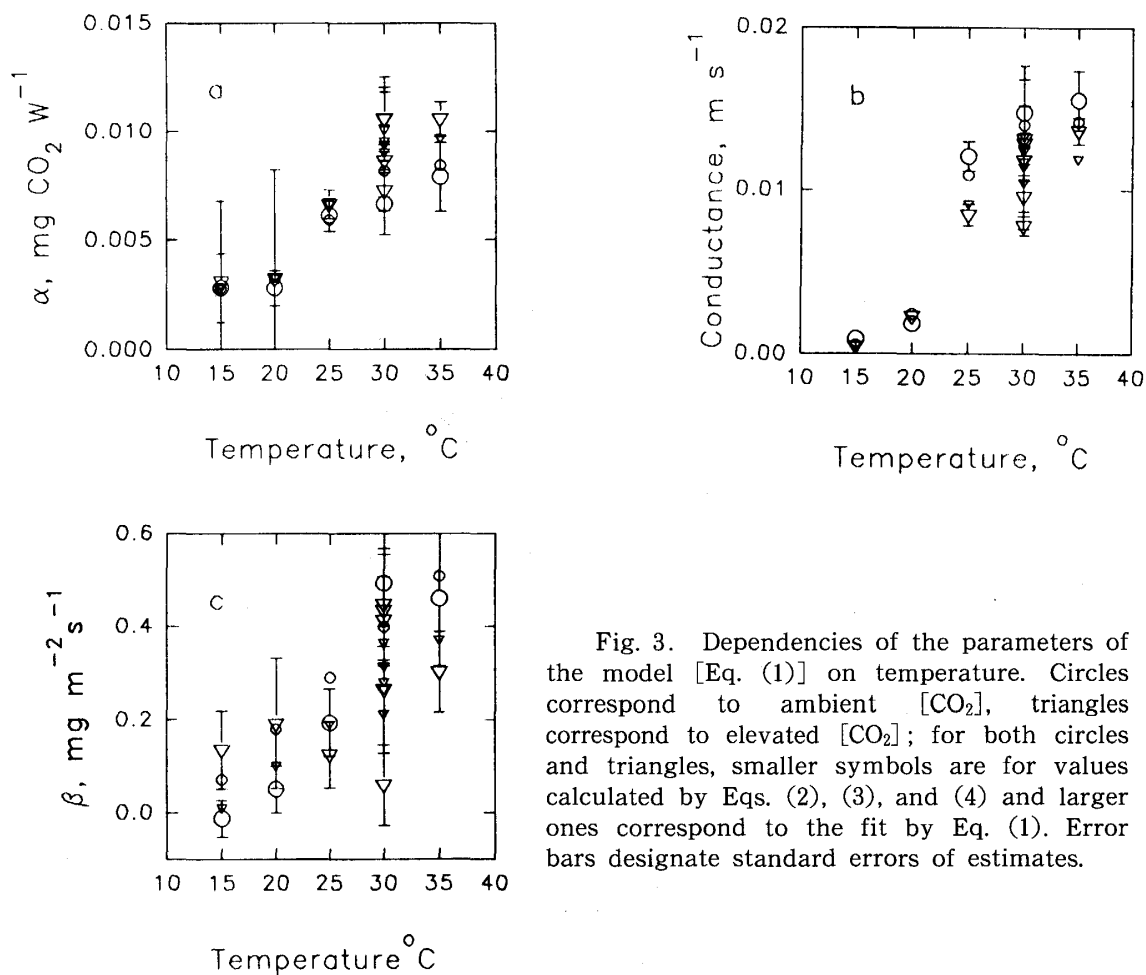


Fig. 3. Dependencies of the parameters of the model [Eq. (1)] on temperature. Circles correspond to ambient $[CO_2]$, triangles correspond to elevated $[CO_2]$; for both circles and triangles, smaller symbols are for values calculated by Eqs. (2), (3), and (4) and larger ones correspond to the fit by Eq. (1). Error bars designate standard errors of estimates.

Table 2. Parameters of the composite CO_2 exchange model as estimated from (a) fitting Eq. (1) to separate light response curves, and (b) fitting the composite model to all light response curves simultaneously.

Parameter	Value	
	a	b
$\alpha_{max, amb} \times 10^3$	8.45	9.23
$\alpha_{min} \times 10^3$	2.76	2.40
$T_{50, \alpha} \times 10^{-1}$	2.46	2.58
q_α	1.82	3.30
$b_\alpha \times 10^6$	3.63	1.26
$\tau_{max, amb} \times 10^3$	14.20	14.55
$\tau_{min} \times 10^3$	0.43	0.70
$T_{50, \tau} \times 10^{-1}$	2.40	2.37
q_τ	1.71	1.03
$b_\tau \times 10^6$	6.48	0.00
a_β	0.26	-0.26
$b_\beta \times 10^1$	0.26	-0.26
$c_\beta \times 10^5$	1.12	-1.02

shape as the temperature dependence of α_c . Figure 3b shows that, unlike the α_c values, the values of τ_c tend to decrease with increasing $[\text{CO}_2]$. A logistic approximation was also used to describe the data for τ_c

$$\frac{\tau_{max} - \tau_c}{\tau_{max} - \tau_{min}} = \frac{1}{1 + e^{\frac{T - T_{50,\tau}}{q_\tau}}} \quad (3)$$

where τ_{max} is the upper limit of the τ_c values; τ_{min} is the lower limit of the τ_c values; $T_{50,\tau}$ is the temperature at which the curve has an inflection point and the τ_c value is midway between τ_{max} and τ_{min} ; and q_τ is a steepness factor. We assumed the upper limit τ_{max} to be linearly dependent on $[\text{CO}_2]$ so that $\tau_{max} = \tau_{max,amb} + b_\tau[\text{CO}_2]$. The parameters for Eq. (2) are listed in Table 2. The calculated values of τ_c are compared with estimated averages in Fig. 3b. The correlation coefficient is equal to 0.79.

The estimated averages of the parameter β are depicted in Fig. 3c. Parameter β clearly depends on temperature. To incorporate these features of the dependencies, we selected the nonlinear equation:

$$\beta = a_\beta - (b_\beta - c_\beta[\text{CO}_2])T \quad (4)$$

where a_β , b_β and c_β are constants. Values of the constants are presented in Table 2. Calculated values of β are compared with estimated averages in Fig. 3c. The correlation coefficient is equal to 0.77.

The composite model characterizing the dependence of CO_2 exchange on environmental factors is represented by Eq. (1) with coefficients α_c , τ_c and β dependent on temperature and $[\text{CO}_2]$ according to Eqs. (2), (3), and (4), respectively. Eqs. (1), (2), (3), and (4) seem to reflect properly the shapes of the corresponding dependencies.

The coefficients of Eqs. (2), (3), and (4) were recalculated by fitting the composite model to the entire data set of 796 points for all canopy light response curves. The new values of the coefficients are presented in Table 2. Mean square error of the composite model decreased by 15% after recalculation, and improvement appears to be statistically significant. Correspondence between measured and calculated CO_2 exchange rates is shown in Fig. 4. The F-test showed that the composite model was quantitatively adequate to describe the experimental data.

DISCUSSION

Table 2 allows comparison of the parameter values obtained from fitting Eqns. 2, 3, and 4 to the estimated average parameters of Eq. (1) with those obtained from fitting the composite model to the entire data set as mentioned above. The dependence of canopy conductance on $[\text{CO}_2]$ disappeared in the composite model, and the dependence of light utilization efficiency on $[\text{CO}_2]$ became weaker. The steepness of the temperature dependencies increased for canopy conductance and decreased for light utilization efficiency.

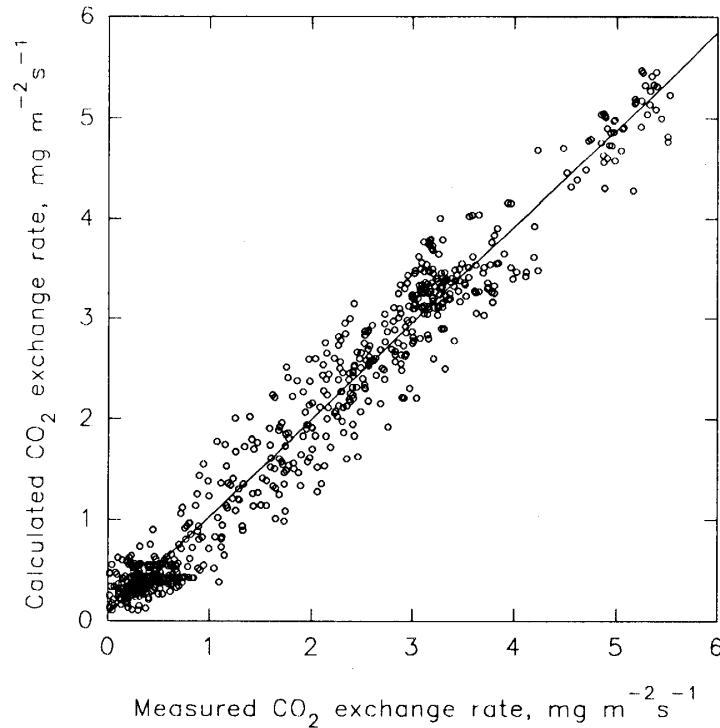


Fig. 4. Comparison of the composite model predictions with the experimental data.

Both light utilization efficiency and conductance to CO₂ transfer can be measured as characteristics of leaf photosynthesis. There is no direct correspondence between these values for leaves and for canopies since leaf conductance, light intensity and other environmental factors vary with depth in the canopy (1). However, it is interesting to compare the dependencies of the CO₂ exchange parameters on environmental factors at two different levels of organization of the plant organism, i. e., at the leaf level and at the canopy level, to assess the validity of modeling of the canopy as a "big leaf."

Leaf light utilization efficiency is a characteristic analogous to the quantum efficiency of photosynthesis (Q_E), which has been measured for the leaves of some species. Published values of Q_E vary from 0.0105 to 0.0148 mg CO₂ W⁻¹ at 330 ppm CO₂, 21% O₂, and 30°C (7, 11, 12). The value of α_c calculated in this study for the light response curve at 350 ppm CO₂ and at a day/night temperature of 30/18°C was 0.01059 mg W⁻¹, i. e. it was close to the lower limit known for Q_E values. When conditions differed from the standard, α_c values in a range of 0.00277 to 0.00584 mg W⁻¹ were found.

Harley and Tenhunen (15) used a constant value of $\alpha_c=0.00875$ mg CO₂ W⁻¹ (0.06 mol CO₂ mol⁻¹ photons) in their crop photosynthesis model. That value is close to the mean α_c value of 0.00696 mg W⁻¹ calculated for the light response curves in the current study. However, one can encounter significant deviations

from the mean caused by temperature and $[\text{CO}_2]$ changes (Table 2). Therefore, the incorporation of temperature and $[\text{CO}_2]$ -dependent parameters can significantly improve the precision of the photosynthesis model.

The dependence of Q_E on $[\text{CO}_2]$ has been pointed out in several publications (10, 11, 17, 22). The quantum efficiency Q_E was shown to be dependent on temperature. The character of the dependence is still uncertain. Harley *et al.* (14) showed that Q_E decreased slightly as temperature decreased over the range of 40 to 25°C with a larger reduction below 15°C. In other experiments under ambient CO_2 and O_2 levels, there was a steady decline in Q_E as temperature increased from 14 to 38°C (10, 11). The current consensus is that α and Q_E are nearly constant under moderate conditions for C_3 plants but that they are sensitive to various stresses, including high and low temperature (6). The dependence of α_c on temperature calculated here demonstrates exactly such a behavior, i.e., optimum plateau in vicinity of the 30–35°C interval. Light utilization efficiency, α_c , expresses the biochemical characteristics of photosynthesis, especially it reflects the carboxylation rate which depends both on temperature and $[\text{CO}_2]$.

Typical values of the leaf conductance to CO_2 transfer lie in the range of 0 to 0.02 m s^{-1} (5, 8). The τ_c values of this study are in this range. The effect of temperature on leaf conductance to CO_2 transfer has been reported in numerous publications (e.g., 8). Lösch and Tenhunen (18) showed that a stomatal aperture maximum in the light was observed at 35°C, with aperture values decreasing at higher and lower temperatures. This is similar to the shape of the dependence of τ_c on temperature in this study.

Leaf conductance to CO_2 transfer is proportional to the stomatal apertures, which are inversely correlated with $[\text{CO}_2]$ (19). This effect may be important in predicting alterations of agricultural productivity caused by global climate change. In contrast to other data on leaf conductance, our results do not show a dependence of canopy conductance on $[\text{CO}_2]$. A mutual compensation of the effects of $[\text{CO}_2]$ and different light intensities across the canopy may be one of the reasons. Another reason might be that τ_c values were found by extrapolation since light saturation was reached in only 4 of the 14 sets of data: at 15/7 and 20/12°C for both 350 and 700 ppm CO_2 . Canopy conductance to CO_2 transfer, τ_c , reflects mostly gas diffusion as a part of the process of photosynthesis. Diffusion depends on temperature and on the gradient of gas concentration between atmosphere and intercellular space. So the dependencies for τ_c calculated here seem reasonable.

CONCLUSIONS

The hyperbolic equation proved to be flexible enough to simulate cotton canopy CO_2 response to variable light intensity at different temperature and $[\text{CO}_2]$ levels. The values of the parameters of the hyperbolic equation increased with increase in temperature. The logistic equation could be used to describe temperature dependencies of both light utilization efficiency and canopy

conductance to CO₂ transfer. Maximum values of both parameters depended linearly on [CO₂]. A combination of the hyperbolic and logistic equations represented the composite model. Re-estimating the parameters of the logistic dependencies significantly improved the overall performance of the composite model. The dependence of canopy conductance on [CO₂] was not evident after parameter re-estimation.

Both canopies and single leaves share some common features of the dependencies of the parameters of the light response hyperbolic model on temperature and [CO₂]. However, information on the response of canopy CO₂ exchange to a changing environment is too scarce, making collection and analysis of this kind of data important.

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