Interactive effects of light, leaf temperature, CO_2 and O_2 on photosynthesis in soybean

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Abstract. A biochemical model of C_3 photosynthesis has been developed by G.D. Farquhar et al. (1980, Planta 149, 78–90) based on Michaelis-Menten kinetics of ribulose-1,5-bisphosphate (RuBP) carboxylase-oxygenase, with a potential RuBP limitation imposed via the Calvin cycle and rates of electron transport. The model presented here is slightly modified so that parameters may be estimated from whole-leaf gas-exchange measurements. Carbon-dioxide response curves of net photosynthesis obtained using soybean plants (*Glycine max* (L.) Merr.) at four partial pressures of oxygen and five leaf temperatures are presented, and a method for estimating the kinetic parameters of RuBP carboxylase-oxygenase, as manifested in vivo, is discussed. The kinetic parameters so obtained compare well with kinetic parameters obtained in vitro, and the model fits to the measured data give r^2 values ranging from 0.87 to 0.98. In addition, equations developed by J.D. Tenhunen et al. (1976, Oecologia 26, 89–100, 101–109) to describe the light and temperature responses of measured CO_2-saturated photosynthetic rates are applied to data collected on soybean. Combining these equations with those describing the kinetics of RuBP carboxylase-oxygenase allows one to model successfully the interactive effects of incident irradiance, leaf temperature, CO_2 and O_2 on whole-leaf photosynthesis. This analytical model may become a useful tool for plant ecologists interested in comparing photosynthetic responses of different C_3 plants or of a single species grown in contrasting environments.

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Introduction

It is our goal to develop an analytical model of whole-leaf photosynthesis, incorporating light and temperature effects, for use as a tool in ecophysiological studies. In particular, we have sought to develop a model, solidly grounded in enzyme kinetics and biochemistry, the parameters of which may be determined solely through analysis of whole-leaf gas-exchange measurements.

Wholephot, developed by Tenhunen et al. (1976a, b, 1977, 1980a), represented an attempt to develop such a model, and has proven useful in simulating daily time courses of net photosynthesis (Tenhunen et al. 1980b, c). However, Harley (1982) has shown that certain assumptions underlying Wholephot are untenable, notably the implicit assumption that ribulose-1,5-bisphosphate (RuBP) concentration is always non-limiting and that the CO_2-saturated rate of CO_2 uptake obtainable in vivo represents the V_{max} of the carboxylating enzyme, RuBP carboxylase-oxygenase.

Farquhar and his colleagues, in a series of papers (Farquhar 1979; Farquhar et al. 1980; von Caemmerer and Farquhar 1981; Farquhar and von Caemmerer 1982), have developed an analytical model of whole-leaf photosynthesis, based on enzyme kinetics, whole-chain electron transport and the energy requirements of the Calvin cycle. In common with other recent modeling efforts, including Wholephot, this model assumes that CO_2 and O_2 compete for RuBP at the enzyme RuBP carboxylase-oxygenase, but, unlike Wholephot, it

does not assume that the concentration of RuBP is saturating under all conditions.

In the model of Farquhar et al., whether or not RuBP is saturating is determined by the complex interaction between the rate of RuBP utilization in carboxylation and oxygenation and the rate of RuBP regeneration via the integrated photosynthetic carbon reduction (PCR), photorespiratory carbon oxidation (PCO) and photorespiratory nitrogen cycles. The rate of substrate regeneration is dependent on the concentrations of ATP and-or reduced NADPH, which are in turn dependent on photosynthetic photon-flux density (PPFD) and rates of whole-chain electron transport.

Farquhar has yet to define ways to determine values of the numerous parameters of the model, short of using values obtained in vitro from isolated chloroplasts or enzymes. Using such values, however, von Caemmerer and Farquhar (1981) were able to generate numerous photosynthetic response curves which behaved realistically. The model presented here is based entirely on the theory described in Farquhar and von Caemmerer (1982), but we have chosen a slightly more empirical approach which allows us to determine, for a given set of environmental conditions, whether or not [RuBP] is limiting. In this way, the characteristics of RuBP carboxylase-oxygenase, as manifested in vivo, may be elucidated from whole-leaf gas-exchange data.

Theory

The reader is referred to Farquhar et al. (1980) and especially Farquhar and von Caemmerer (1982) for a detailed discussion of the mathematical derivation of the model utilized here, and of the assumptions on which it is based.

Farquhar et al. derive two expressions describing net assimilation. Equation (1) describes the case in which RuBP concentration is non-limiting, and assimilation (A) is determined solely by the properties of RuBP carboxylase-oxygenase and the partial pressures of CO_2 and O_2.

$$A = W_c \, (1 - \Gamma_*/C) - R_d^1 \tag{1}$$

where C is the intercellular partial pressure of CO_2 and R_d is the rate of respiration continuing in the light, here termed residual respiration. W_c is the RuBP saturated rate of carboxylation described by

$$W_c = Vc_{max} \cdot \frac{C}{C + K_c(1 + O/K_o)} \tag{2}$$

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1 Symbols and units are listed at the end of this article

where Vc_{max} is the maximum carboxylation velocity, K_c and K_o are the Michaelis constants for CO_2 and O_2, respectively, and O is the partial pressure of O_2. Γ_* in eqn. (1) is the CO_2 compensation point in the absence of residual respiration and may be expressed,

$$\Gamma_* = \frac{0.5 \, Vo_{max}K_c}{Vc_{max}K_o} \cdot O \tag{3}$$

where Vo_{max} is the maximum oxygenation velocity. Equation (4) describes net assimilation when the regeneration of RuBP limits the potential assimilation rate.

$$A = J'(1 - \Gamma_*/C) - R_d \tag{4}$$

where J' is the electron transport-photophosphorylation-limited rate of carboxylation. The actual assimilation rate under a given set of conditions is the minimum of eqns. (1) and (4), expressed,

$$A = (1 - \Gamma_*/C) \cdot \min\{W_c, J'\} - R_d \tag{5}$$

where "min { }" denotes "minimum of".

Farquhar et al. (1982) presented several alternative expressions to describe J', depending on whether NADPH or ATP is limiting the rate of RuBP regeneration, and whether additional ATP is generated via cyclic electron transport, the Mehler reaction or DHAP-PGA shuttle. Assuming that NADPH is limiting RuBP regeneration, or that additional ATP are generated in cyclic electron transport,

$$J' = \frac{JC}{4C + 8\Gamma_*} \tag{6}$$

where J is the potential rate of whole-chain electron transport. In this paper, we introduce a parameter, P_m, the measured gross photosynthesis rate at saturating partial pressures of CO_2, representing therefore the maximum potential rate of carbon assimilation under given conditions of irradiance and temperature. If NADPH is limiting RuBP regeneration and RuBP regeneration is limiting carbon assimilation, 2 mol of NADPH and 4 mol of electrons are needed for each mol of carbon reduced, i.e., 4 P_m is equal to J, and

$$A = (1 - \Gamma_*/C) \cdot \min\left\{W_c, \frac{P_m C}{C + 2\Gamma_*}\right\} - R_d. \tag{7}$$

Material and methods

Seeds of soybean (*Glycine max* (L.) Merr.) cv. P 61–22 (Pioneer Hy-bred, Des Moines, Ia., USA) were sown in vermiculite inside an environmental growth cabinet (model E8VH; Conviron, Winnipeg, Man., Canada) and watered with distilled water. On the ninth day after planting, healthy seedlings were trans-

planted into 12.5-cm plastic pots containing a 50:50 (v/v) mixture of coarse vermiculite and perlite (both from Grace Horticultural Products, Cambridge, Mass., USA). After transplanting, the plants were watered to field capacity twice daily with 0.5-strength Hoagland's solution (after Wagner and Cumming 1970), and grown under a 16-h photoperiod and a day/night temperature regime of 30/20° C, with temperatures raised in the morning and lowered in the evening in 1-h-long 2° C increments. Maximum PPFD at a height of 23 cm was maintained between 0.8 and 1.0 mmol (photons) $m^{-2} s^{-1}$.

All measurements were conducted on the terminal leaflet of the second trifoliate leaf. The photosynthetic capacity of a soybean leaf increases during early development, reaching a maximum at approximately the time of full leaf expansion, and subsequently declines (Woodward 1976; Ojima et al. 1965). Under the growth regime employed, full expansion and maximum photosynthetic capacity of the second trifoliate leaf were attained an average of 22 d after planting (data not shown). All gas-exchange data reported here were obtained on plants between 21 and 23 d of age.

Gas exchange of intact leaves was measured using an infrared gas analyzer (Series Five; Sensors, Ann Arbor, Mich., USA) in an open, flow-through gas-exchange system described in detail in Harley (1982). Experimental gases were obtained by cascading pure CO_2, O_2 and N_2 through a series of gas-mixing pumps (H. Wösthoff, Bochum, FRG). The dewpoint of the gas entering and leaving the assimilation chamber was measured using a dew-point hygrometer (model 880; EG & G, International, Waltham, Mass., USA). Photon-flux densities up to 3.0 mmol $m^{-2} s^{-1}$ were obtained using a 400-W metal-halide lamp (Powerstar; Osram, West Berlin, FRG), and the flow rate of the gas through the assimilation chamber was measured using a mass-flow meter (ALL-5K; Teledyne-Hastings-Raydist, Hampton, Va., USA). Leaf area measurements were made using a portable area meter (LI-3000; LI-COR, Omaha, Neb., USA).

The assimilation chamber was a cylinder of 6-mm-thick plexiglass, 115 mm in diameter and 32 mm deep, provided with water jackets above and below. Leaf temperatures could be maintained within ±0.2° C and were measured using a copper-constantan 36-gauge (0.127-mm) thermocouple. Incident PPFD was measured with a small silicon cell, calibrated against a factory-calibrated quantum sensor (LI-192; LI-COR). A small fan insured adequate gas mixing within the assimilation chamber. Measured absorption of water and CO_2 by the assimilation chamber was negligible at the flow rates used.

Rates of transpiration and net photosynthesis were calculated using the equations of von Caemmerer and Farquhar (1981), incorporating corrections for dilution of the gas stream with transpired water vapor.

In the analysis portion of this paper, it is necessary to fit complex functions to measured data. All such curve fitting has been performed by non-linear least-squares regression analysis (Draper and Smith 1966), using a statistical program, BMDX85 (Dixon 1969), provided by the University of Michigan Statistical Laboratory (Ann Arbor, Mich., USA). Initial estimates of the parameter values and a subroutine containing the derivatives of the function to be fit with respect to each parameter must be provided.

Results and analysis

Equation (7), used to describe net photosynthesis, contains five parameters, four of which (Vc_{max}, Vo_{max}, K_c and K_o) describe the kinetic properties of RuBP carboxylase-oxygenase, as manifested in
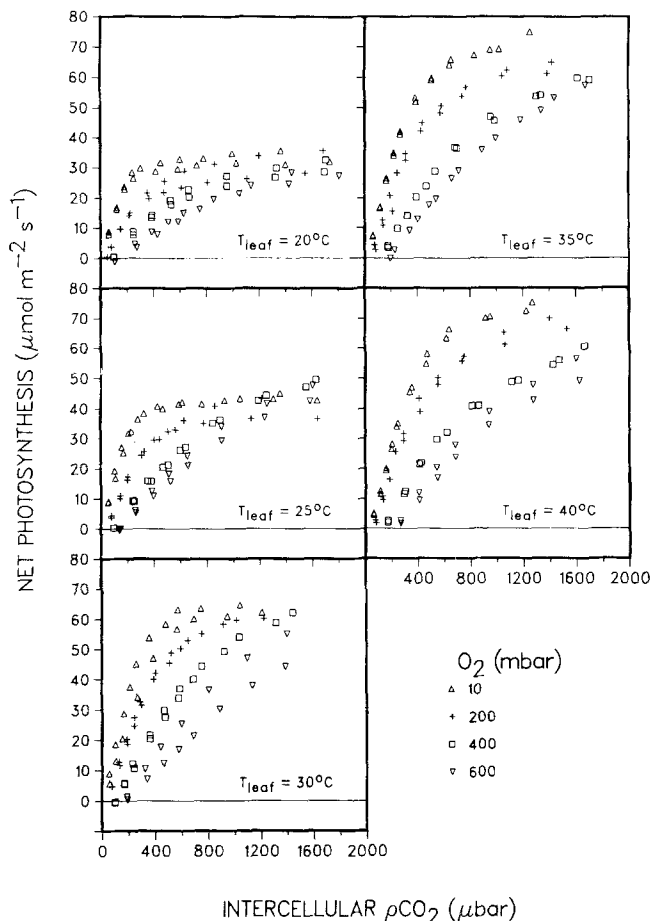

Fig. 1. Net photosynthesis in soybean as a function of internal $p(CO_2)$ at four $p(O_2)$ and five leaf temperatures. PPFD was greater than 2.0 mmol $m^{-2} s^{-1}$

vivo, and a fifth, P_m, representing the CO_2-saturated rate of gross photosynthesis. The determination of values for the kinetic parameters and for P_m will be treated separately.

1) Determination of kinetic parameters. In order to develop a data set for the determination of values for the kinetic parameters discussed above, a family of CO_2 response curves of net photosynthesis was obtained at each of five leaf temperatures between 20° and 40° C (Fig. 1). Each family of curves consisted of two replicates at each of four $p(O_2)$ (approx. 10, 200, 400, and 600 mbar). Each individual curve in Fig. 1 was obtained on a different leaf, and leaf-to-leaf variation accounts for the scatter in the data.

A primary controlling step of the integrated PCR and PCO cycles occurs at RuBP carboxylase-oxygenase, where CO_2 and O_2 compete for RuBP following competitive Michaelis-Menten kinetics. Were RuBP never limiting, classic enzymological

techniques, such as double-reciprocal plots, might be applied to whole-leaf gas-exchange data such as those in Fig. 1. As shown by Lilley and Walker (1975) and Ku and Edwards (1977), however, double-reciprocal plots deviate drastically from linearity as $p(CO_2)$ increases, indicating that RuBP concentration is limiting the reaction under such conditions.

Von Caemmerer and Farquhar (1981), based on theoretical analysis of RuBP utilization in carboxylation-oxygenation and RuBP production via electron transport and the Calvin cycle, suggest that RuBP concentration becomes limiting at CO_2 partial pressures of 220 μbar or less in *Phaseolus vulgaris* at 28° C and saturating photon-flux densities. Current estimates of the $Km(CO_2)$ of RuBP carboxylase, obtained in vitro at 25° C, cluster between 250 and 600 μbar (Badger and Andrews 1974; Jensen and Bahr 1977; Jordan and Ogren 1981; Laing et al. 1974; Yeoh et al. 1981), with recent estimates of Seemann et al. (1981) and Seemann and Berry (1982) falling on the low end of that range. This indicates that RuBP may well become limiting at $p(CO_2)$ at or below that required for half-saturation of the carboxylase reaction. In such a case, attempts to estimate kinetic parameters from whole-leaf gas-exchange data by means of double-reciprocal plots seem impractical since the range of CO_2 used may fall below the $Km(CO_2)$ of the enzyme (Segel 1975). Ku and Edwards (1977) and Monson et al. (1982), however, have applied this method with some success. Another method of estimating kinetic parameters is presented below.

Any attempt to determine kinetic parameters will be valid only if all data used in the analysis are obtained under conditions in which RuBP is non-limiting. Since the exact $p(CO_2)$ at which RuBP becomes limiting cannot be determined a priori, we have arbitrarily assumed that those points on each curve in Fig. 1 obtained at the four lowest $p(CO_2)$ represent such data (Fig. 2). Note that none of the responses has begun to curve significantly over this region, as would be expected were RuBP to become seriously limiting. Furthermore, for the curves obtained at 10 mbar O_2, all data are obtained at $p(CO_2)$ below 250 μbar, which compares well with the aforementioned estimate (von Caemmerer and Farquhar 1981) of the approximate $p(CO_2)$ at which RuBP becomes limiting.

At present, it is impossible to measure R_d, and the question of whether respiration continues in the light, and if so at what rate, remains controversial. Initially, we assume R_d is zero; subsequently,
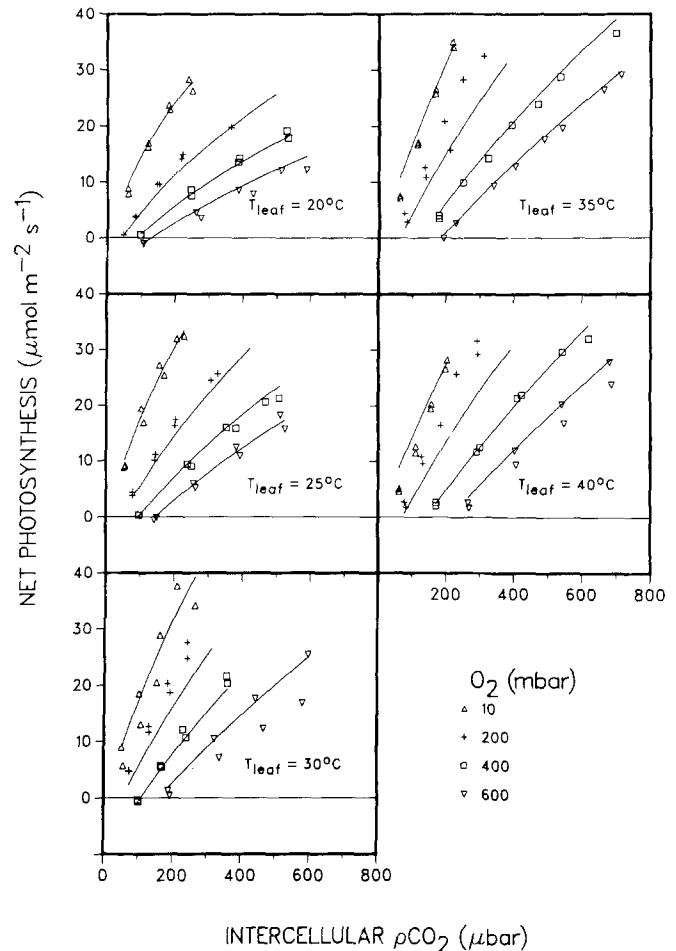

INTERCELLULAR pCO_2 (μbar)

Fig. 2. Net photosynthesis in soybean as a function of internal $p(CO_2)$ at four $p(O_2)$ and five leaf temperatures. PPFD was greater than 2.0 mmol m^{-2} s^{-1} and RuBP is assumed to be non-limiting. *Solid lines* are least-squares fits to eqn. (8), using parameter values found in Table 5

we will adopt the other extreme and assume dark respiration continues unabated in the light. Assuming RuBP is not limiting the reaction, the expression "$\min\left\{W_c, \dfrac{P_m C}{C + 2\Gamma_*}\right\}$" in eqn. (7) takes on the value of W_c. Setting R_d equal to zero, substituting for W_c (eqn. 2) and Γ_* (eqn. 3), eqn. (7) can be rearranged, yielding

$$A = \frac{C \cdot K_o V c_{max} - 0.5 \cdot K_c V o_{max} O}{K_c O + K_c K_o + K_o C}. \tag{8}$$

Each of the five families of curves in Fig. 2 was fit independently to eqn. (8), using non-linear least-squares methodology (BMDX85) (Dixon 1969). The parameter estimates obtained are found in Table 1. As might be expected when trying to fit such a complex data set exhibiting considerable internal scatter, and when iterating for four parameters simultaneously, the standard deviations of several

Table 1. Best least-squares estimates and SD of the parameters Vc_{max}, K_c, Vc_{max} and K_o in soybean

Leaf temp. (°C)	Vc_{max} (μmol m^{-2} s^{-1})	K_c (μbar)	Vo_{max} (μmol m^{-2} s^{-1})	K_o (mbar)	$\dfrac{Vo_{max}}{Vc_{max}}$
20	68.7 ± 11.5	339 ± 86	15.0 ± 2.6	168.3 ± 16.3	0.22
25	101.5 ± 22.4	441 ± 133	22.8 ± 4.0	209.0 ± 19.0	0.22
30	97.5 ± 42.6	413 ± 254	40.5 ± 18.1	328.3 ± 90.3	0.41
35	155.1 ± 81.8	759 ± 487	40.4 ± 16.8	336.2 ± 73.4	0.26
40	152.8 ± 151.1	903 ± 1044	62.1 ± 49.4	530.3 ± 278.4	0.41

parameter estimates are quite large (e.g., at 35° and 40° C). Nevertheless, the fit of predicted to measured rates is quite good, with r^2 values ranging from 0.87 to 0.98, where r^2 represents the proportion of the Sum of Squares Total explained by eqn. (8).

There is a healthy tendency to question parameter values obtained using non-linear least-squares methodology, particularly when as many as four parameters are iterated for simultaneously. It seems likely that there is more than one set of parameter estimates which would provide good fits to the measured data and meet the criteria of the least-squares program. This fact and the large standard-deviation values in Table 1 led us to reduce the number of parameters iterated for, which may be done in several ways.

K_o may be eliminated from consideration as follows. Equation (3), which implies that Γ_* is a linear function of oxygen concentration with slope equal to $0.5\,K_c Vo_{max}/K_o Vc_{max}$, has been used frequently (Laing et al. 1974; Tenhunen et al. 1980a; Farquhar and von Caemmerer 1982). The value of Γ_* was determined by regression for each curve in Fig. 2, and Γ_* as a function of $p(O_2)$ is plotted for a leaf temperature of 25° C in Fig. 3 (triangles, line A). Included in Fig. 3 is a linear regression fit to these data. The slope of this line and of the lines obtained at the other experimental temperatures are found in Table 2 (column headed P_n). These slopes are plotted as a function of leaf temperature and fit to a linear regression in Fig. 4 (triangles, line A), resulting in the following expression:

$$\frac{0.5\,K_c Vo_{max}}{K_o Vc_{max}} = 0.00680\,T_{leaf} + 0.0722. \qquad (9)$$

Rearranging, and solving for K_o,

$$K_o = \frac{1}{0.0136\,T_{leaf} + 0.144} \cdot \frac{Vo_{max}K_c}{Vc_{max}}. \qquad (10)$$

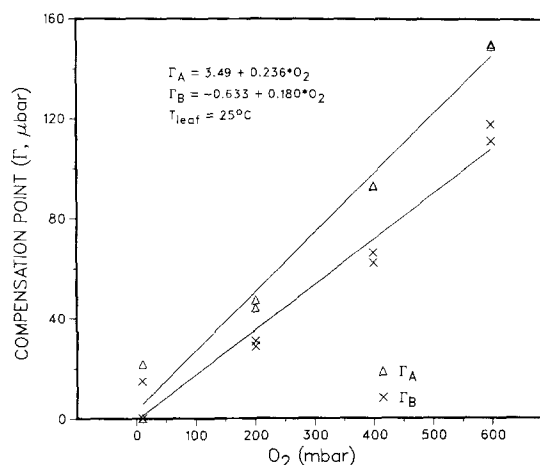Substituting this expression into eqn. (8) eliminates the parameter K_o from consideration. Using

Fig. 3. CO_2 compensation point (Γ) of soybean as a function of $p(O_2)$ at 25° C, based on either net photosynthesis data ($\triangle$) or net photosynthesis plus residual respiration ($\times$). *Solid lines* are linear fits to the data, using equations shown

Table 2. Slope of the relationship between CO_2 compensation point (Γ) and oxygen concentration as a function of leaf temperature in soybean. Values in column 1 are based on net photosynthesis data (Pn), those in column 2 on data to which dark respiration has been added (Pg)

Leaf temp. (°C)	Slope (Pn) (μbar CO_2/mbar O_2)	Slope (Pg) (μbar CO_2/mbar O_2)
20	0.214	0.149
25	0.236	0.189
30	0.282	0.232
35	0.294	0.243
40	0.355	0.294

BMDX85, each data set in Fig. 2 was fitted to this modified version of eqn. (8), and new best least-squares estimates of the three remaining parameters obtained, as shown in Table 3. Although the standard deviations of the estimates are somewhat reduced compared with the values in Table 1, they remain rather large.

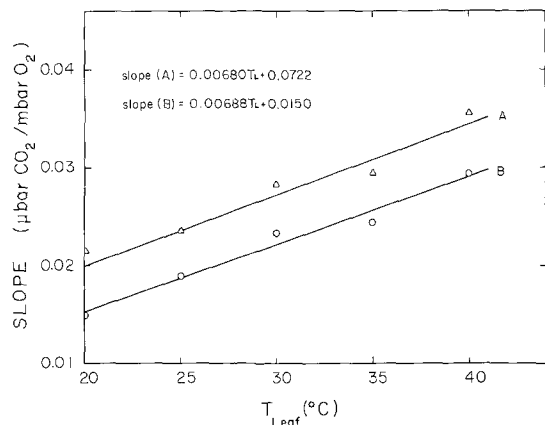Another way to eliminate a parameter from consideration is to adopt the assumption made by

Fig. 4. Slope of the relationship between CO_2 compensation point (Γ) and oxygen as a function of leaf temperature in soybean, using values in Table 2, based either on net photosynthesis data (Δ) or net photosynthesis plus residual respiration (o). *Solid lines* are linear fits to the data, using equations shown

Farquhar and von Caemmerer (1982), based on in vitro kinetic data of Badger and Andrews (1974) and Badger and Collatz (1977), that the ratio of Vo_{max} to Vc_{max} is virtually constant and approx. 0.21. Substituting this equality into eqn. (8) eliminates Vo_{max}. BMDX85 was again used to fit the data sets in Fig. 2 to eqn. (8) and the resulting parameter estimates are found in Table 4. Note that requiring Vo_{max} to be held as a constant proportion of Vc_{max} reduces substantially the standard deviations of the parameter estimates.

Finally, both of the restrictions imposed above were imposed simultaneously, i.e., Vo_{max} was set equal to 0.21 Vc_{max} and K_o was restricted according to eqn. (10). Two parameters having been eliminated from consideration, BMDX85 iterated for those values of Vc_{max} and K_c which provided the best least-squares fit to the five data sets in Fig. 2. These parameter estimates are found in Table 5, and the solid lines in Fig. 2 represent the fit to the data sets based on these parameter values. In fact, however, fits to these data using parameter values in Tables 1, 3 and 4 are virtually indistinguishable from those shown.

It has been assumed to this point that CO_2 release in the light from non-photorespiratory processes is negligible, i.e., R_d is zero. In the following, we adopt the other extreme and assume that R_d is equivalent to dark respiration which continues unabated in the light.

Measured rates of dark respiration as a function of leaf temperatures are shown in Fig. 5 (triangles). Using BMDX85, these data were fit to eqn. (11), a simple Arrhenius function,

$$R_d = e^{(c - E/RT_k)} \qquad (11)$$

where e is the base of the natural logarithm, c is a constant, E is the activation energy (J mol^{-1}), T_k is the leaf temperature (°K), and R is the gas constant (8.31 J °K^{-1} mol^{-1}). The resulting fit and parameter values appear in Fig. 5. Assuming that dark respiration continues in the light, the

Table 3. Best least-squares estimates and SD of the parameters Vc_{max}, K_c and Vo_{max}, obtained using BMDX85. Values of K_o are restricted according to eqn. (10)

| Leaf temp. (°C)	Vc_{max} (μmol m^{-2} s^{-1})	K_c (μbar)	Vo_{max} (μmol m^{-2} s^{-1})	K_o (mbar)	$\dfrac{Vo_{max}}{Vc_{max}}$
20	69.3 ± 11.3	343 ± 85	14.5 ± 1.0	166.7	0.21
25	101.0 ± 20.7	438 ± 124	23.1 ± 1.7	209.9	0.23
30	95.4 ± 38.2	401 ± 228	43.1 ± 9.4	338.3	0.45
35	144.0 ± 56.9	693 ± 339	44.6 ± 8.0	352.0	0.31
40	140.7 ± 97.7	819 ± 675	68.6 ± 27.8	564.1	0.49

Table 4. Best least-squares estimates and SD of the parameters Vc_{max}, K_c and K_o, obtained using BMDX85. Vo_{max} was assumed to be 0.21 Vc_{max}

Leaf temp. (°C)	Vc_{max} (μmol m^{-2} s^{-1})	K_c (μbar)	Vo_{max} (μmol m^{-2} s^{-1})	K_o (mbar)	$\dfrac{Vo_{max}}{Vc_{max}}$
20	70.1 ± 6.3	349 ± 50	14.7	167.8 ± 15.6	0.21
25	105.5 ± 9.6	464 ± 61	22.1	207.8 ± 17.6	0.21
30	140.7 ± 35.1	669 ± 222	29.5	295.4 ± 64.8	0.21
35	175.5 ± 26.6	880 ± 171	36.8	322.7 ± 40.6	0.21
40	229.2 ± 54.3	1 429 ± 411	48.1	456.6 ± 91.7	0.21

Table 5. Best least-squares estimates and SD of the parameters Vc_{max} and K_c, obtained using BMDX85. K_o is restricted according to eqn. (10), and Vo_{max} is restricted to 0.21 Vc_{max}

Leaf temp. (°C)	Vc_{max} (μmol m^{-2} s^{-1})	K_c (μbar)	Vo_{max} (μmol m^{-2} s^{-1})	K_o (mbar)	$\dfrac{Vo_{max}}{Vc_{max}}$
20	69.0 ± 2.6	341 ± 26	14.5	166.3	0.21
25	107.8 ± 4.0	478 ± 32	22.6	210.3	0.21
30	169.5 ± 18.6	838 ± 144	35.6	328.7	0.21
35	191.7 ± 12.3	973 ± 106	40.3	335.1	0.21
40	259.6 ± 28.3	1 632 ± 283	54.5	484.2	0.21
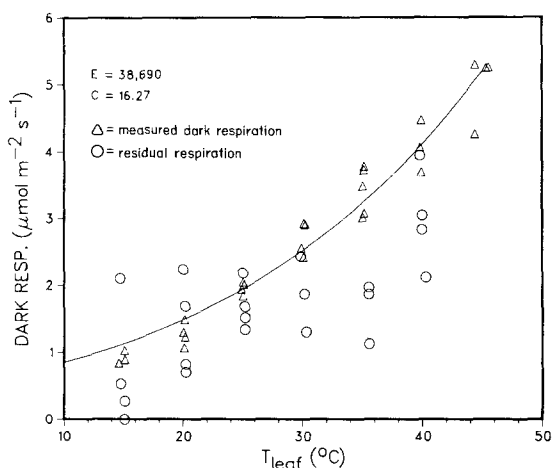
Fig. 5. Comparison between measured dark respiration ($\triangle$) and estimated residual respiration (o) in soybean as a function of leaf temperature. *Solid line* is least-squares fit of dark respiration to eqn. (11) using parameter values shown. E in J mol^{-1}

appropriate value of R_d from eqn. (11) was added back to each curve shown in Figs. 1 and 2. Adding back R_d to the data obviously alters the relationship between Γ_* and oxygen concentration. New values of Γ_* were obtained by regression using this modified data set, and those obtained at 25° C may be seen in Fig. 3 (× symbols). The slope of this relationship and the slopes at the other measurement temperatures are given in Table 2, and the slopes as a function of leaf temperature are plotted in Fig. 4 (circles, line B). A linear fit to

these data gives the equation shown in the figure. Rearranging,

$$K_o = \frac{1}{0.01376\, T_{leaf} + 0.030} \cdot \frac{Vo_{max}K_c}{Vc_{max}}. \qquad (12)$$

Restricting Vo_{max} to 0.21 Vc_{max} and restricting K_o to the value given by eqn. (12), these new data sets with R_d added were fit to eqn. (8), and the best least-squares estimates of Vc_{max} and K_c are given in Table 6. The fits to the data (not shown) are virtually the same as in the previous analysis, but the parameter values are uniformly reduced.

2) Description of the P_m surface. In order to determine the light and temperature dependencies of the CO_2-saturated rate of photosynthetic uptake, P_m, a single light-response curve of net photosynthesis was obtained from each of 24 leaves, at leaf temperatures ranging from 15° to 40° C (Fig. 6). Internal $p(CO_2)$ was saturating or very nearly so (> 1000 μbar), and $p(O_2)$ was 10 μbar.

The initial portion of the light-response curve is apparently linear (Tenhunen et al. 1976a), and the initial slope, here designated α, represents the maximum efficiency of light-energy conversion (Chartier 1970), based on incident PPFD. Following Tenhunen et al. (1976b), a linear regression was applied to the lowest three points of each light-response curve. The slope of the regression line provides an estimate of α, and the y-intercept of

Table 6. Best least-squares estimates and SD of the parameters Vc_{max} and K_c obtained using BMDX85. K_o is restricted according to eqn. (12), and Vo_{max} is restricted to 0.21 Vc_{max}. R_d added back to data

Leaf temp. (°C)	Vc_{max} (μmol m^{-2} s^{-1})	K_c (μbar)	Vo_{max} (μmol m^{-2} s^{-1})	K_o (mbar)	$\dfrac{Vo_{max}}{Vc_{max}}$
20	56.2 ± 1.9	220 ± 18	11.8	146.1	0.21
25	87.2 ± 2.8	318 ± 21	18.3	185.1	0.21
30	137.8 ± 12.6	572 ± 91	28.9	286.2	0.21
35	169.0 ± 9.3	720 ± 72	35.5	301.4	0.21
40	247.2 ± 22.6	1 254 ± 191	51.9	422.2	0.21

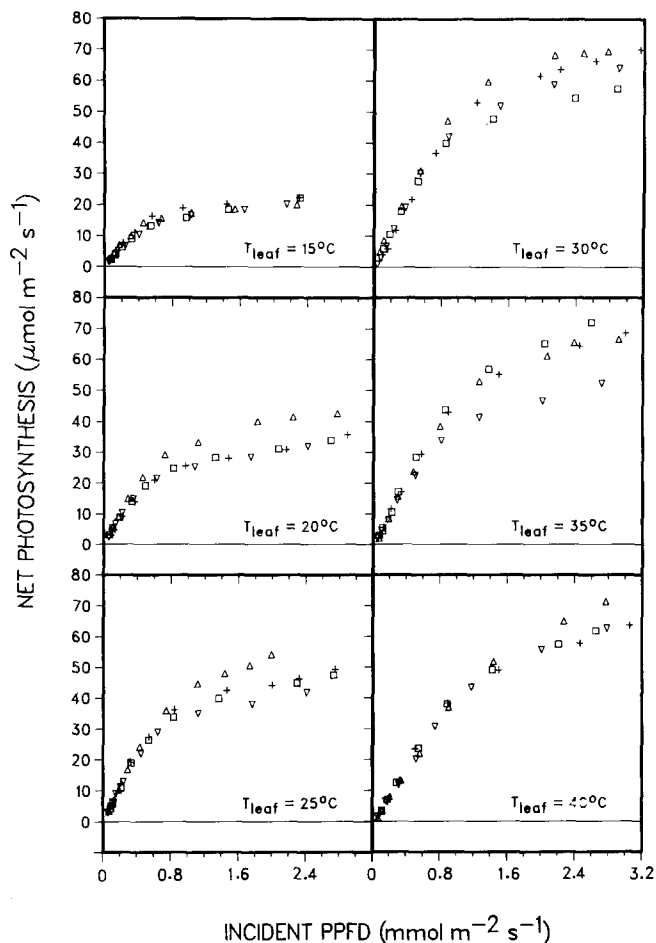**Fig. 6.** Net photosynthesis in soybean as a function of incident PPFD at six leaf temperatures. $p(CO_2)$ is greater than 1000 µbar and $p(O_2)$ is 10 mbar

Table 7. Values of residual respiration and α in soybean, based on either a three-point linear regression or the higher estimate of a three-point regression and a four-point binomial regression

Leaf temp. (°C)	Residual respiration (μmol m^{-2} s^{-1})		Initial slope (α) (mmol mol (photons)$^{-1}$)	
	Three-point	High est.	Three-point	High est.
15.5	0.72	2.10	44.4	68.6
15.5	0.00	0.26	33.0	44.5
15.0	0.17	0.55	30.7	37.4
15.5	0.00	0.00	27.2	34.9
20.0	0.25	1.74	53.9	71.2
20.0	1.27	2.20	47.3	61.4
20.0	0.00	0.69	47.6	60.9
20.0	0.62	0.79	52.6	56.4
25.0	1.33	1.33	63.2	63.2
25.0	0.98	2.18	68.3	95.2
25.0	1.44	1.67	65.6	68.6
25.0	1.50	1.50	61.1	61.1
30.0	0.00	0.00	56.1	60.5
30.0	1.34	1.34	49.7	49.7
30.0	1.24	2.44	59.7	72.1
30.0	1.94	1.94	58.7	58.7
35.0	3.05	3.05	61.4	61.4
35.0	1.94	1.94	56.1	56.1
35.0	1.97	1.97	61.3	61.3
35.0	1.07	1.12	53.3	53.6
40.0	2.47	3.07	50.4	61.0
40.0	2.91	2.91	51.2	51.2
40.0	3.02	4.03	53.9	65.0
40.0	1.88	2.09	53.4	57.0
Mean values of $\alpha \pm$ SD			52.5 $\pm$ 10.5	59.6 $\pm$ 12.0

the regression, i.e., light equal to zero, provides an estimate of residual respiration (Table 7).

If the light response of photosynthesis is not precisely linear over this range, i.e., if the response has begun to curve towards saturation, values of α and residual respiration obtained in this way will necessarily be underestimates. To guard against this possibility, a binomial regression of the lowest four points of each curve was used to estimate α and residual respiration recalculated. The higher of these two estimates of both α and residual respiration (Table 7) are used in subsequent analysis.

Inasmuch as it is analogous to quantum efficiency, α should theoretically be independent of temperature, and indeed above 15° C, it appears to be so (Fig. 7). The unexpected drop in α at 15° C may perhaps be explained as the result of low-temperature-induced changes in photosynthetic membrane structure or permeability (Raison 1974; Pike and Berry 1979; Berry and Björkman 1980),
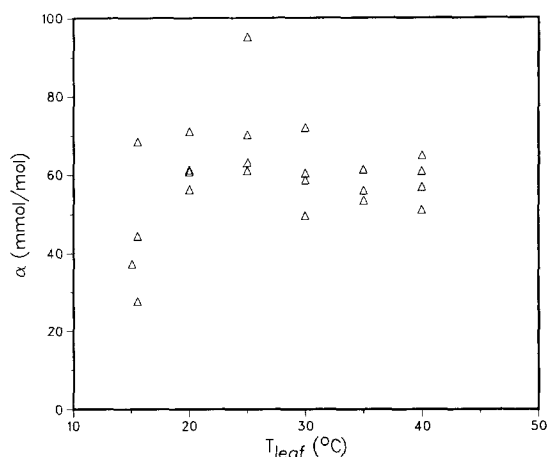

Fig. 7. Estimates of α, the initial slope of the light response, as a function of leaf temperature in soybean

though 15° C seems rather high for such changes to occur, even for plants grown under a 30/20° C day/night temperature regime. The mean value of α, based on all the data in Fig. 7, is 59.6 $\pm$ 12.0 mmol mol (photons)$^{-1}$ ($n = 24$). Based only
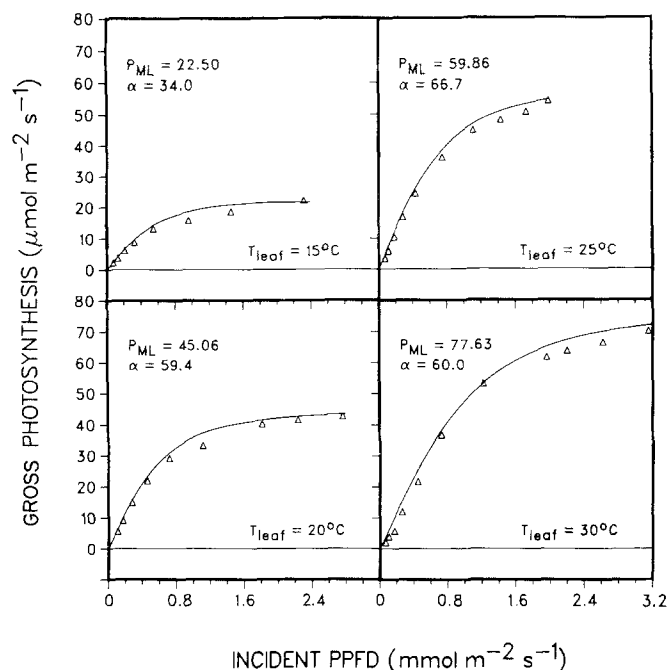
Fig. 8. Gross photosynthesis of soybean as a function of incident PPFD for individual curves at four leaf temperatures. *Solid lines* are least-squares fits to eqn. (13), using parameter values shown

on data above 15° C, the mean value of α equals 62.3 ± 9.7 ($n=20$), which compares well with the mean value of 73.3 obtained by Ehleringer and Björkman (1977), expressed on the basis of absorbed rather than incident quanta. This implies an absorptance for our leaves (not measured) of approx. 80%.

The high degree of scatter notwithstanding, values of residual respiration are comparable to measured mitochondrial respiration in the dark, and residual respiration increases with temperature in a manner similar to dark respiration (Fig. 5). For the sake of simplicity, therefore, residual respiration again is considered to be mitochondrial respiration continuing unabated in the light, and the temperature dependency of residual respiration will be defined as the temperature dependency of measured dark respiration (Fig. 5). Whether or not mitochondrial respiration continues in the light, and if so at what rate, remain controversial questions (Graham and Chapman 1979; Graham 1980; Sharpe et al. 1984). However, inasmuch as residual respiration in this study averages less than 6% of photosynthetic uptake, any error introduced at this stage will be relatively small.

The light-response curves in Fig. 6 were transformed from net to gross photosynthesis by adding to each curve the appropriate temperature-dependent rate of residual respiration, using eqn. (11)

Table 8. BMDX85 estimates of α and P_{ml} which provide the best least-squares fit to eqn. (5), and best-fit estimates of P_{ml} when α is restricted to a mean value of 57.6 mmol mol (photons)$^{-1}$

Leaf temp. (°C)	Both α and P_{ml} calculated in BMDX85		P_{ml} calculated in BMDX85; $\alpha = 57.6$
	α (mmol mol (photons)$^{-1}$)	P_{ml} (μmol m^{-2} s^{-1})	P_{ml} (μmol m^{-2} s^{-1})
15.5	46.4	20.74	19.82
15.5	43.6	23.45	21.97
15.0	34.0	22.50	19.61
15.5	34.9	21.42	18.96
20.0	59.4	45.06	45.39
20.0	46.6	35.55	33.80
20.0	53.0	34.64	34.00
20.0	55.6	32.37	32.12
25.0	66.7	59.86	63.95
25.0	67.6	43.64	45.49
25.0	68.6	50.74	52.76
25.0	64.8	49.59	51.10
30.0	72.4	78.39	85.02
30.0	60.0	77.63	78.77
30.0	66.8	61.71	64.37
30.0	63.7	69.67	72.28
35.0	62.7	76.12	78.52
35.0	63.4	76.31	79.01
35.0	66.8	81.42	87.60
35.0	60.5	56.73	57.65
40.0	50.8	87.84	81.92
40.0	57.0	71.05	70.78
40.0	57.0	71.87	71.55
40.0	52.8	74.07	71.13
($\bar{\alpha}=57.6$)			

and the parameter values shown in Fig. 5. Tenhunen et al. (1976 b) obtained excellent fits to light-response curves of gross photosynthesis under CO_2-saturating conditions (P_m) using an empirical equation developed by Smith (1937), which will be used here.

$$P_m = \frac{\alpha I}{\left(1 + \dfrac{\alpha^2 I^2}{P_{ml}^2}\right)^{1/2}} \tag{13}$$

where: α is the maximum efficiency of light energy conversion, i.e., the initial slope (mmol mol (photons)$^{-1}$); P_{ml} is the photosynthetic rate at saturating irradiance, saturating CO_2, and a specific leaf temperature (μmol m^{-2} s^{-1}); I is the photosynthetic photon flux density (mmol m^{-2} s^{-1}). Using BMDX85, each curve was fitted independently to eqn. (13); four representative fits are shown in Fig. 8. Best-fit estimates of α and P_{ml} are given in Table 8. For the purpose of modeling, it was
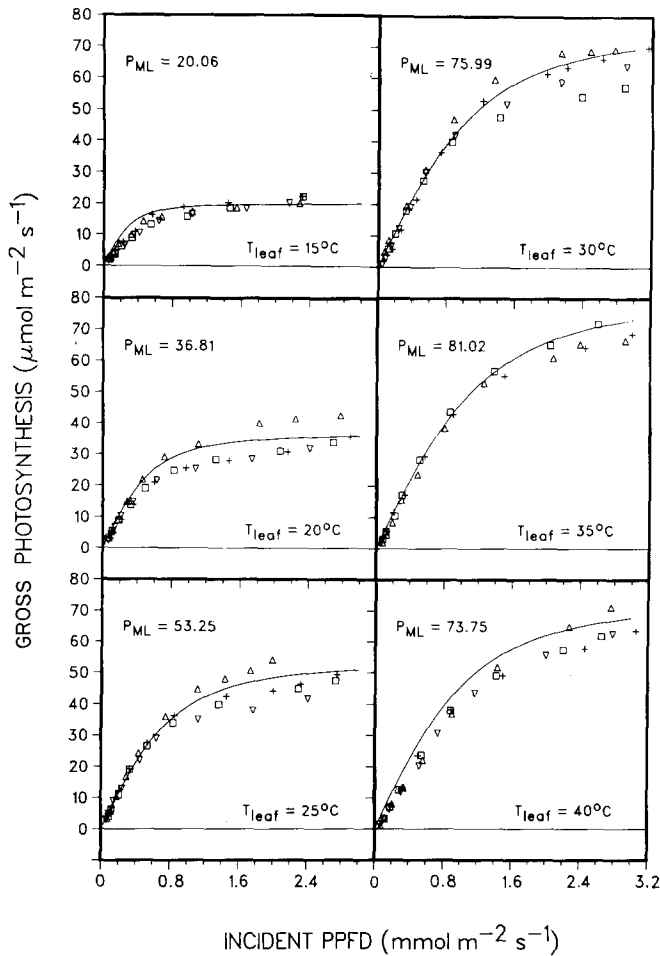
Fig. 9. Gross photosynthesis of soybean as a function of incident light intensity at six leaf temperatures. *Solid lines* are least-squares fits to eqn. (13), using parameter values shown. α is fixed at 57.6 mmol mol^{-1} (photons)

Fig. 10. Estimates of the CO_2- and light-saturated rates of gross photosynthesis in soybean (P_{ML}), obtained using BMDX85, as a function of leaf temperature. *Solid line* is a least-sqares fit to eqn. (14), using parameter values shown. ΔH_a and ΔH_d are in J mol^{-1}, and ΔS is in J K^{-1} mol^{-1}

necessary to establish a constant value for α, and the mean value of 57.6 mmol mol^{-1} in Table 8 was used. Having established a constant value for α, a second set of fits to eqn. (13) were obtained using BMDX85, in which the value of α was fixed at 57.6, resulting in new best-fit estimates of P_{ml} (Table 8). Finally, light-response data were aggregated by leaf temperature and, with α fixed at 57.6, each set of four curves was fit to eqn. (13) (Fig. 9). (Note that the response curve at 35° C with its anomalously low maximum rate of 57.65 was removed from the analysis at this time.) Estimates of P_{ml} obtained on individual curves (triangles) and on data aggregated by temperature (circles) are plotted as a function of leaf temperature in Fig. 10.

As demonstrated by Tenhunen et al. (1976b), these data may be described by an equation developed by Johnson et al. (1942) to describe the temperature response of enzyme activity where activa-
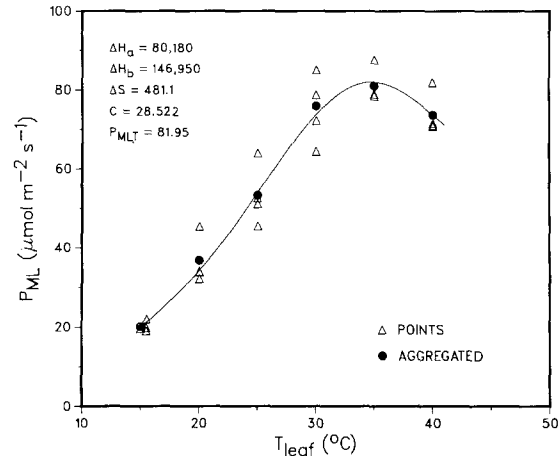
tion of the enzyme and high-temperature inactivation of the enzyme are assumed to be the only two processes involved. This equation has also been used by Sharpe and DeMichele (1977), Hall (1979) and Farquhar et al. (1980) to describe similar processes. In a form slightly modified from that used by Tenhunen, the equation is:

$$P_{ml} = \frac{T_K \cdot e^{(c - \Delta H_a/RT_K)}}{1 + e^{(\Delta S T_K - \Delta H_d)/(RT_K)}} \qquad (14)$$

where: c is a constant, ΔH_a is the activation energy for the reaction (J mol^{-1}), ΔH_d is the activation energy for the denaturation equilibrium (J mol^{-1}), and ΔS is the entropy of the denaturation equilibrium (J °K^{-1} mol^{-1}). The data points in Fig. 10 were fitted to eqn. (14) using BMDX85, and the resulting fit is given by the solid line, using best-fit parameter estimates as shown.

Thus, combining eqns. (13) and (14), it is possible to construct a three-dimensional surface which quite accurately describes gross photosynthesis under CO_2-saturating conditions as a function of both incident PPFD and leaf temperature. Such a surface, designated the P_m surface, is shown in Fig. 11, based on the parameter estimates obtained above.

3) Integration of P_m surface and kinetic parameters. Combining the light and temperature dependencies of P_m and the temperature dependency of R_d with the kinetic parameters arrived at previously, we can describe the photosynthetic response to CO_2 concentration in both the RuBP-saturated and RuBP-limited portions of the curve. Using eqns.
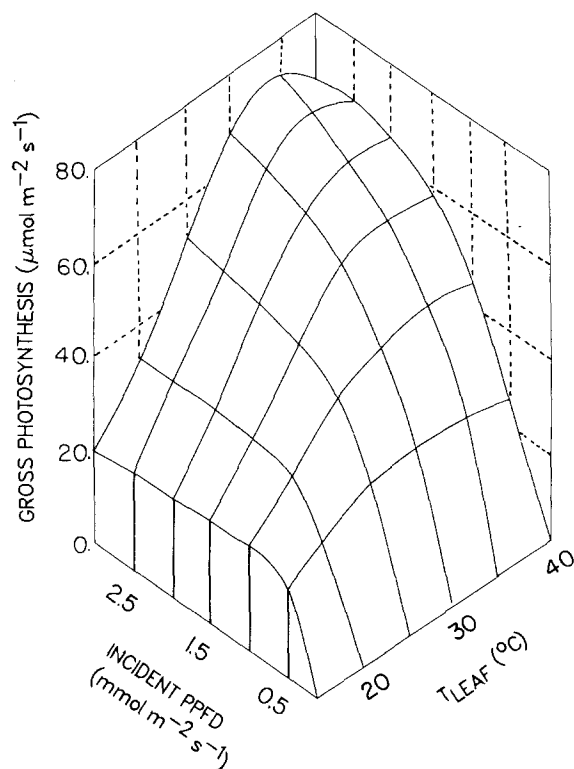
Fig. 11. Three-dimensional representation of CO_2-saturated rates of gross photosynthesis (P_m) of soybean as a function of both incident PPFD and leaf temperature, based on parameter values found in Figs. 9 and 10

INTERCELLULAR pCO_2 (μbar)

Fig. 12. Net photosynthesis of soybean as a function of internal $p(CO_2)$ at four $p(O_2)$ and five leaf temperatures. The PPFD is greater than 2.0 mmol m^{-2} s^{-1}. *Solid lines* are based on eqn. (7)

(7), (13) and (14) and the parameter values in Tables 6 and 8, simulation curves were generated using as inputs the $p(CO_2)$, $p(O_2)$, PPFD and leaf temperature values for the CO_2-response curves in Fig. 1. These simulations are compared with the measured data in Fig. 12. The abrupt change in slope of each curve represents the $p(CO_2)$ at which RuBP becomes limiting in simulation, i.e., the point at which W_c equals $\dfrac{P_m C}{C + 2\Gamma_*}$ in eqn. (7). It was assumed in the kinetic analysis that the lowest four points of each response curve represented data under conditions where RuBP concentration was non-limiting. Figure 12 confirms that, within the framework of this model, this assumption is valid.

When interpreting Fig. 12, it should be remembered that the lowest four points were used to obtain the estimates of the kinetic parameters used in this analysis. The lines in Fig. 12 in this low-CO_2 portion of the response, therefore, represent non-linear least-squares fits to those points, rather than independent predictions. Above this region, however, the lines are not fits to data, but predictions based on eqn. (7). In this RuBP-limited portion of the response, the parameters obtained in the above analysis of photosynthetic light-response
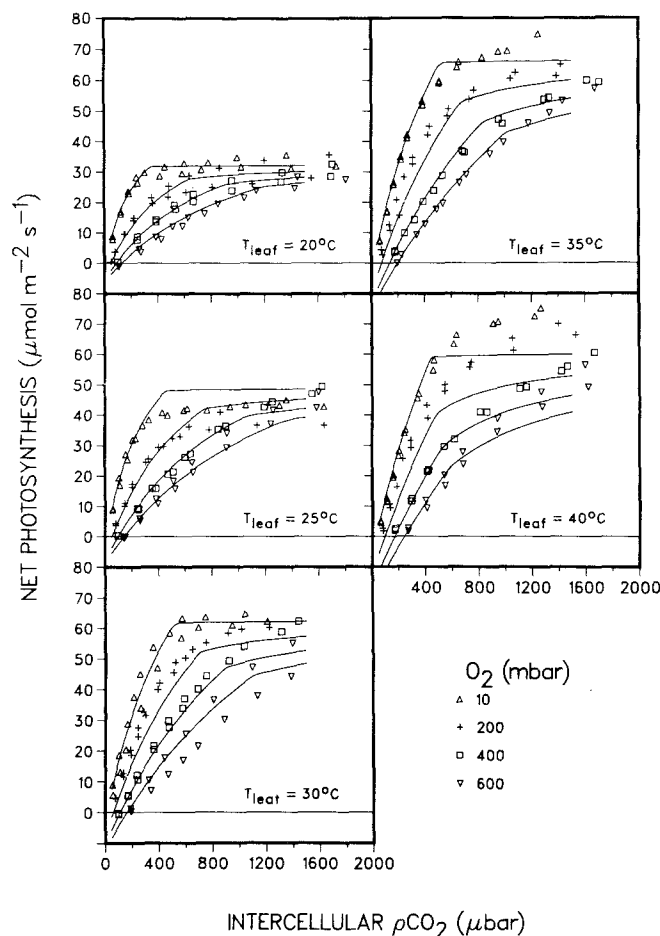
data were used to predict the CO_2 responses of a different set of experimental plants, which explains some of the disparity between measured and predicted rates at high $p(CO_2)$. This is particularly evident at 25° C and 40° C, where the ceilings imposed on the response by RuBP regeneration are clearly too high and too low respectively. Despite these difficulties, the overall agreement between measured and predicted rates is encouraging.

In a further attempt to utilize model parameters generated above to simulate an independently measured data set, two CO_2-response curves were obtained at a leaf temperature of 30° C and an incident PPFD of 0.8 mmol m^{-2} s^{-1}, the approximate conditions during growth (Fig. 13). The model response under these conditions (solid line) is again encouraging, though underestimating slightly the RuBP-limited portion of the response. The dotted line in the figure represents the supply function for CO_2 (Farquhar and Sharkey 1982), based on
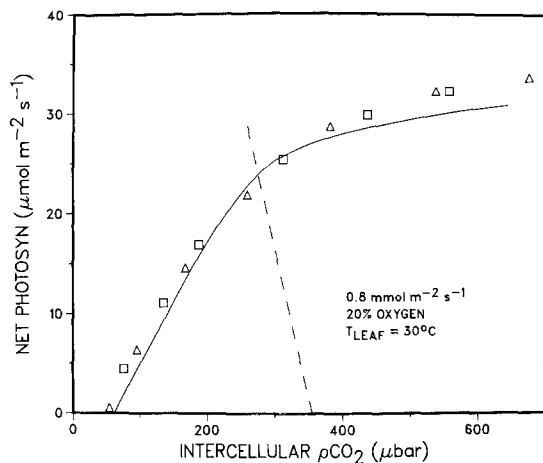
Fig. 13. Net photosynthesis of two soybean leaves as a function of internal $p(CO_2)$ measured at 200 mbar O_2 and incident PPFD of 0.8 mmol m^{-2} s^{-1}. Solid line is predicted photosynthesis, based on eqn. (7). Dotted line is the CO_2 supply function of Farquhar and Sharkey (1982), based on stomatal conductance to CO_2 of 0.4 mol m^{-2} s^{-1}

an average measured conductance at ambient CO_2 of 0.4 mol m^{-2} s^{-1}, and it is interesting to note that the point at which this function intercepts the demand function, measured under conditions approximating those under which the plants were grown, is very near the point of transition between the carboxylase-limited and the RuBP-limited portions of the response. A similar situation was observed by von Caemmerer and Farquhar (1981), and as discussed by Farquhar and Sharkey (1982) represents optimal water use as well as an optimal distribution of nitrogen between RuBP carboxylase-oxygenase and the machinery for RuBP regeneration, such that neither occurs in substantial excess.

Discussion

Farquhar et al. (1980) and von Caemmerer and Farquhar (1981) demonstrated the feasibility of modeling whole-leaf photosynthesis according to competitive Michaelis-Menten kinetics, where it is assumed that, at low intercellular $p(CO_2)$ and high light intensity, assimilation is limited by the RuBP-saturated rate of RuBP carboxylase-oxygenase activity. As either $p(CO_2)$ is increased or light intensity decreased, it is further assumed that the rate of assimilation becomes limited by the rate of regeneration of RuBP. Adopting published values of in-vitro kinetic parameters for RuBP carboxylase-oxygenase as well as literature values for maximum rates of electron transport, they were able to generate numerous photosynthetic response

curves which behaved in a realistic fashion, and elucidated the ways in which incident light intensity, leaf temperature, $p(CO_2)$ and $p(O_2)$ interact in the photosynthetic response.

The research reported here represents an attempt to apply these ideas to an experimentally obtained data set, from which the necessary parameter values may be obtained directly, without recourse to either in-vitro enzyme studies or measurements made on isolated chloroplasts.

This initial attempt to determine, in vivo, values for the kinetic parameters in eqns. (2) and (3) is encouraging. The values of K_c and K_o in Table 5, where residual respiration is assumed to be zero, and in Table 6, where it is assumed equal to dark respiration, fall well within the range of values reported from in-vitro studies. At 25° C, for example, the K_c values in Tables 5 and 6 are 478 and 318 µbar, respectively. Converted to units of molarity, these become 15.7 and 10.5 µM dissolved CO_2, which compare well with published values of Jordan and Ogren (1981) ($\bar{x} \simeq 12.6$ µM; $n = 5$), Jensen and Bahr (1977) ($\bar{x} \simeq 17.5$ µM; $n = 7$), Yeoh et al. (1981) ($\bar{x} \simeq 19.3$ µM; $n = 28$), Seemann et al. (1981) and Seemann and Berry (1982) ($\bar{x} \simeq 10.4$ µM; $n = 4$). Similarly, the values given for K_o at 25° C in Tables 5 and 6, 210 and 185 mbar, expressed as dissolved oxygen, become 258 and 227 µM, falling between values cited by Jensen and Bahr (1977) (208 µM) and Jordan and Ogren (1981) (532 µM). Given the considerable scatter in estimates of kinetic parameters obtained in vitro, the estimates obtained here in vivo are well within acceptable limits.

Though the kinetic parameters obtained on a variety of C_3 species by Jordan and Ogren (1981) showed considerable variation, their "substrate specificity factor", defined as $Vc_{max}K_o/Vo_{max}K_c$, showed remarkable stability across species, averaging 80.0 at 25° C. Using the parameter estimates in Tables 5 and 6, concentrations converted to molarities, one obtains values at 25° C of 78.3 and 102.9, respectively. If values for the "substrate specificity factor" are calculated at the other measurement temperatures, the "specificity factor" decreases with increasing temperature (data not shown). Inasmuch as this ratio represents the relative rates of carboxylation and oxygenation, this decline demonstrates the oft-cited response of photorespiration (oxygenation) being increasingly favored with increasing temperature (Laing et al. 1974; Badger and Collatz 1977).

The question of whether CO_2 release in the light by processes other than the PCO cycle comprises an appreciable part of CO_2 exchange in vivo

remains unresolved (Graham and Chapman 1979; Graham 1980). Assuming that measured dark respiration continues unabated in the light (Table 6) does not affect the fits of predicted to measured rates, but it does force the kinetic parameters down towards the lower limit of reported values mentioned above. Given the relatively large percentage of heterotrophic tissue in the leaf (Jellings and Leech 1982), which is expected to be unaffected by light, the extreme assumption adopted here of zero residual respiration seems unlikely (see also Sharpe et al. 1984). Similarly, evidence for the suppression of respiration in autotrophic cells in the light (Graham 1980), while not unequivocal, indicates that the alternative assumption adopted here, that dark respiration continues unabated in the light, seems equally unlikely. If actual residual CO_2 release in the light lies somewhere between these extremes, parameters would assume values intermediate to those in Tables 5 and 6.

An analytical model, of course, is only as good as the set of assumptions underlying it. The primary assumption on which this model is based is that carbon assimilation is controlled by the kinetics of RuBP carboxylase-oxygenase and the concentrations of its substrates, CO_2, O_2 and RuBP at the site of fixation, and that the enzyme is fully activated. That the enzyme is, in fact, fully activated under all conditions is unlikely, as both low $p(CO_2)$ (Lorimer et al. 1976) and low irradiance (Perchorowicz et al. 1981) appear to cause partial inactivation. Farquhar and von Caemmerer (1982) calculate the effective CO_2 Michaelis constant for enzyme activation as approx. 10 µbar at high irradiance, in which case the enzyme may be assumed to be totally CO_2 activated under the conditions employed in this study. Perchorowicz et al. (1981) suggest that reduced enzyme activation limits whole-leaf CO_2 uptake in wheat seedlings under conditions of limiting light. Under the high irradiances employed in this study, the enzyme should be fully activated; however, for lower irradiances, this question may have to be re-evaluated.

A second, implicit, assumption is that the calculated $p(CO_2)$ in the intercellular air space is identical to that at the site of fixation. Clearly, this is unrealistic inasmuch as a concentration gradient must exist in order for CO_2 flux to continue. Farquhar and von Caemmerer (1982) discuss this problem and make a convincing argument that the expected concentration drop between the intercellular air space and the site of fixation is likely to be relatively small, on the order of 10-15% at ambient CO_2 levels and high photosynthesis rates.

Finally, the assumption made in determining

kinetic parameters that the ratio of Vo_{max} to Vc_{max} is constant at 0.21 seems to have only slight experimental foundation. That the ratio is indeed constant seems likely, given that the two reactions occur at the same active site and have very similar activation energies (Badger and Collatz 1977). More in-vitro evidence is necessary, however, before a specific value for the ratio can be relied upon. It should be mentioned that varying the value of that ratio in this analysis does not significantly affect the fit of predicted to measured data; however, reducing the ratio from 0.21 to 0.17, for example, increases the estimates of both Vc_{max} and K_c by approx. 20%.

Although the procedures outlined in this study involve the accumulation of considerable gas exchange data in order to obtain model parameters, we believe that models of this kind represent an important advance in our ability to understand the kinetics of CO_2 exchange at the level of the whole leaf, and that they substantially enhance our ability to make ecophysiological comparisons between species or between plants acclimated to different environments. The extent to which certain parameters may be considered constants for C_3 species remains to be seen. Hall (1979) discusses potential applications for models of whole-leaf photosynthesis, as well as practical considerations in applying such models to plants in natural environments. He suggests that such parameters as α (on an absorbed quanta basis), K_c and K_o may be relatively constant. And we endorse the suggestion of Farquhar and von Caemmerer (1982) that changes in Vc_{max} (proportional to total RuBP carboxylase-oxygenase) and their parameter J_{max} (equivalent to $4P_{ml}$), along with changes in rates of dark respiration may determine changes in the overall photosynthetic response to environment. Further studies such as this one, carried out on different species or on plants experiencing different growth conditions, will help determine the validity of such suggestions.

Symbols and units

α (mmol mol^{-1})	maximum efficiency of light energy conversion
A (µmol m^{-2} s^{-1})	rate of net assimilation of CO_2
C (µbar)	intercellular partial pressure of CO_2
E (J mol^{-1})	activation energy for respiration
Γ_* (µbar)	CO_2 compensation point in absence of residual respiration

ΔH_a (J mol^{-1})   activation energy for CO_2 and light-saturated assimilation

ΔH_d (J mol^{-1})   activation energy for denaturation equilibrium of CO_2 and light-saturated assimilation

I (mmol m^{-2} s^{-1})   incident irradiance

J (μEq m^{-2} s^{-1})   potential rate of electron transport

J' (μEq m^{-2} s^{-1})   electron-transport limit on rate of carboxylation

K_c (μbar)   Michaelis constant for CO_2

K_o (mbar)   Michaelis constant for O_2

O (mbar)   partial pressure of O_2

P_m (μmol m^{-2} s^{-1})   assimilation rate at saturating CO_2

P_{ml} (μmol m^{-2} s^{-1})   assimilation rate at saturating CO_2 and irradiance

R (J °K^{-1} mol^{-1})   gas constant

R_d (μmol m^{-2} s^{-1})   rate of dark respiration or residual respiration in the light

ΔS (J °K^{-1} mol^{-1})   entropy of the denaturation equilibrium of CO_2 and light saturated assimilation

Vc_{max} (μmol m^{-2} s^{-1})   maximum carboxylation velocity

Vo_{max} (μmol m^{-2} s^{-1})   maximum oxygenation velocity

W_c (μmol m^{-2} s^{-1})   RuBP-saturated rate of carboxylation

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