A Model Describing Photosynthesis in Terms of Gas Diffusion and Enzyme Kinetics

PAUL W. LOMMEN, CHRISTA R. SCHWINTZER, C. S. YOCUM* and DAVID M. GATES

Missouri Botanical Garden, St. Louis

Summary. A model predicting net photosynthesis of individual plant leaves for a variety of environmental conditions has been developed. It is based on an electrical analogue describing gas diffusion from the free atmosphere to the sites of CO_2 fixation and a Michaelis-Menten equation describing CO_2 fixation. The model is presented in two versions, a simplified form without respiration and a more complex form including respiration. Both versions include terms for light and temperature dependence of CO_2 fixation and light control of stomatal resistance. The second version also includes terms for temperature, light, and oxygen dependence of respiration and O_2 dependence of CO_2 fixation.

The model is illustrated with curves based on representative values of the various environmental and biological parameters. These curves relate net photosynthesis to light intensity, $[CO_2]$, $[O_2]$, temperature, and resistances to CO_2 uptake. The shape of the $[CO_2]$-net photosynthesis curves depends on the total diffusion resistance to CO_2 uptake and the Michaelis constant for CO_2 uptake. The curves range from typical Michaelis-Menten to Blackman types.

The model is combined with a model of leaf energy exchange permitting simultaneous estimation of net photosynthesis and transpiration. The combined model is illustrated with curves relating transpiration to photosynthesis under a wide variety of environmental conditions. Environmental regimes yielding maximum efficiency of water use are identified for the given assumptions and biological parameters.

Introduction

Net fixation of CO_2 by plants is governed by a complex series of interactions of biological and environmental factors. These act on two basic processes, gas diffusion to the sites of carbon fixation and the biochemical processes of carbon fixation. We have developed a mathematical photosynthesis model for a leaf that combines descriptions of these basic processes and clearly shows the interaction between them. The model may be used by itself to help solve a variety of physiological problems. For example, it can be used to show the relative importance of any one factor, e.g. light intensity, in determining the rate of photo-

---

* On leave of absence from: Department of Botany, The University of Michigan, Ann Arbor, Michigan 48104, USA.

synthesis under a given set of conditions. The model is combined with an equation describing the leaf energy budget to calculate the simultaneous rates of transpiration and photosynthesis for a given set of environmental conditions. This permits examination of a variety of ecologically important relationships. For example, the efficiency of water use (the ratio of photosynthesis to transpiration) can be estimated for any given set of biological and environmental conditions.

Two versions of the model are presented. First we give a simplified version for plants that do not respire in the light; later we give a somewhat more complex version including a respiratory source of CO_2 for plants that respire in the light.

The Model

A. Simplified Version for Leaves which do not Respire in Light

Both this version and the standard version presented in the next section are based on two fundamental relationships. First, the physical process of CO_2 diffusing from the atmosphere to the site of CO_2 fixation in the chloroplast is described by Fick's Law:

$$P = \frac{C_A - C_C}{R} \tag{1}$$

where: P is the photosynthetic rate (nM cm^{-2} s^{-1})*
C_A is the [CO_2] in the air (nM cm^{-3})
C_C is the [CO_2] in the chloroplasts (nM cm^{-3})
R is the resistance to CO_2 diffusion from the air through the leaf boundary layer, stomata, intercellular air spaces, cell walls and cytoplasm into the chloroplasts (s cm^{-1}).

Second, the chemical process of CO_2 fixation is described by an equation in the form of the Michaelis-Menten equation (M-M eq.) for the rate of an enzymatic reaction (this is not a true Michaelis-Menten case since a series of reactions is involved):

$$P = \frac{P_M}{1 + \dfrac{K}{C_C}} \tag{2}$$

where: P_M is the rate of photosynthesis (nM cm^{-2} s^{-1}) at saturating C_C
K is a constant equal to the chloroplast concentration of CO_2 (nM cm^{-3}) at which $P = P_M/2$.

Eq. (1) is solved for C_C, substituted into Eq. (2), and the resulting quadratic equation solved for P. Thus,

---

* nM = nanomoles.

$$P = \frac{(C_A + K + R P_M) - [(C_A + K + R P_M)^2 - 4 C_A R P_M]^{\frac{1}{2}}}{2R}. \tag{3}$$

Mathematical details regarding this equation are in Appendix B. Further, using Eq. (3) it can be shown that

$$\lim_{R \to \infty} P = \frac{C_A}{R} \tag{4}$$

that is, at high values of resistance, every CO_2 molecule reaching the chloroplasts is fixed so quickly that C_C is essentially zero. Thus the rate of CO_2 diffusion determines the photosynthetic rate for large R. Also,

$$\lim_{R \to 0} P = \frac{P_M}{1 + \dfrac{K}{C_A}} \tag{5}$$

that is, at very low resistance the rate of photosynthesis is determined by the rate of the biochemical processes of CO_2 fixation.

Thus if our assumptions are valid and the M-M eq. accurately describes the fixation of CO_2 in the chloroplasts then Eq. (3) accurately describes the photosynthesis of a nonrespiring leaf in the light. Eq. (3) does not contain a term for dark respiration on the simplifying assumption that dark respiration is completely suppressed in the light even at low light intensities. Since it lacks a term for dark respiration, it can not be applied in the dark.

The maximum rate of photosynthesis (P_M) is a function of light intensity and leaf temperature (T). The light intensity dependence is described with another M-M eq.:

$$P_M(L) = \frac{P_{ML}}{1 + \dfrac{K_L}{L}} \tag{6}$$

where: P_{ML} is the value of P_M at light saturation (nM cm^{-2} s^{-1})

L　is the light intensity between 400 and 700 nm (erg cm^{-2} s^{-1})

K_L　is the light intensity (erg cm^{-2} s^{-1}) at which $P_M(L) = P_{ML}/2$.

The temperature dependence of P_M has the same general characteristics as that of other biochemical processes. In Fig. 1 we show $G(T)$, G as a function of T, a temperature dependence of P_M which we later use for illustration. It was adapted from the temperature dependence of net photosynthesis of a moss (Rastorfer and Higinbotham, 1968) after examination of the temperature dependence of net photosynthesis of a variety of plants including several vascular plants (Raschke, 1970; Hofstra and Hesketh, 1969; Saitoh et al., 1970). Thus, we have for L and T dependencies of P_M

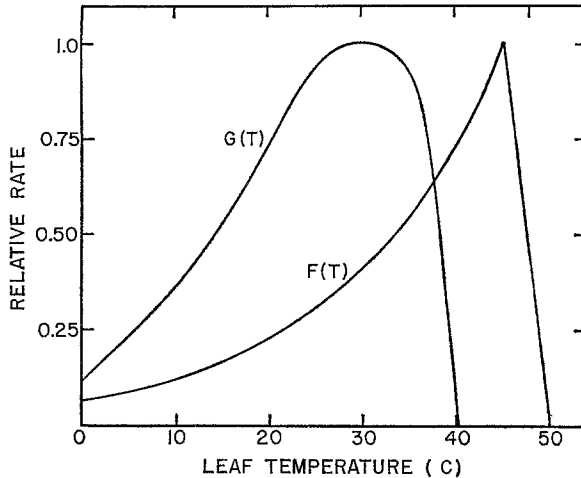$$P_M(L, T) = \frac{P_{MLT} \, G(T)}{1 + \dfrac{K_L}{L}} \tag{7}$$

Fig. 1. Relative values of the maximum rate of photosynthesis, $G(T)$, and the maximum rate of dark respiration, $F(T)$, as functions of leaf temperature. The values are based on data in Figs. 1 and 2 of Rastorfer and Higinbotham (1968) for *Bryum sandbergii* at light intensities of 1.2×10^5 erg cm^{-2} s^{-1} (wavelength distribution not given) and 3.0% CO_2 in air. Values for dark respiration at $T > 39°$C are estimates

where: P_{MLT} is the value of P_M at saturation L and optimum T (nM cm^{-2} s^{-1}).

From the data of Gaastra (1959) K_L is seen to be about 1×10^5 erg cm^{-2} s^{-1}. The three forms of P_M are related to each other as follows: P_M is the maximim photosynthesis rate attainable at saturating C_C and a given light intensity and temperature; P_{ML} is the maximim rate attainable at saturing C_C and saturating light at a given temperature; and P_{MLT} is the maximum rate attainable by the leaf at saturating C_C, saturating light, and optimum temperature.

The temperature dependence of K and K_L is not at all certain. The value of K is determined by the ratio of the sum of the rate constants of the two reactions leading to the disappearance of the enzyme-substrate complex and the rate constant for its formation (Briggs and Haldane, 1925) in one more steps of the CO_2 reduction cycle. Each rate constant is expected to be temperature dependent. If their relative T dependencies are the same, K will be independent of T. Since data are not very complete on this, we will assume, for purposes of illustration at least, that $dK/dT = 0$.

The value of K_L is determined by the light reactions of photosynthesis and may be determined either by the photoacts or by the
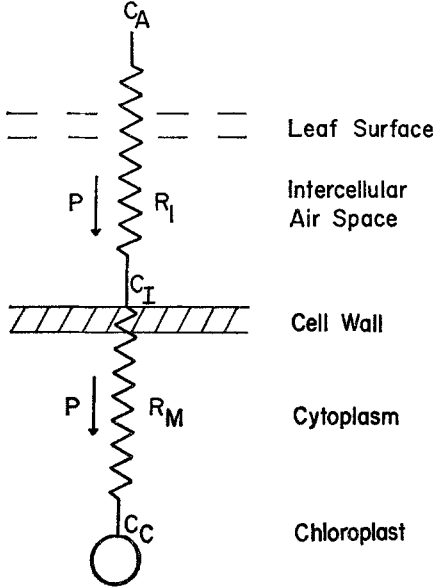
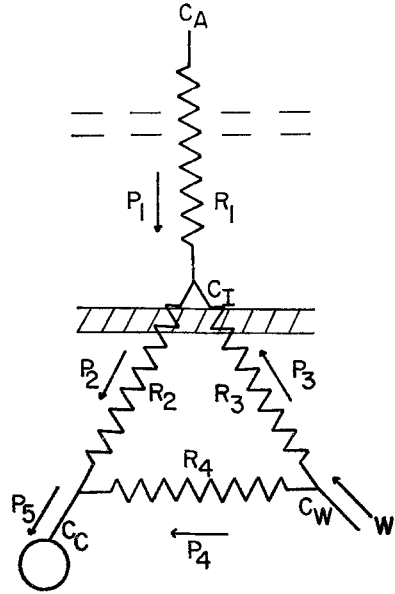A. Without Respiration   B. With Respiration

Fig. 2 A and B. Electrical analogues of CO_2 exchange in leaves. A. Simplified resistance network without a respiratory source of CO_2. B. Standard resistance network including a respiratory source of CO_2. Fluxes are taken as positive when they are in the directions indicated by the arrows. The R's are resistances, P's are CO_2 fluxes, and C's are CO_2 concentrations. All symbols are defined in Appendix A

associated enzymatic steps. In the first case, it is temperature independent and in the latter the same arguments apply as in the case of K.

The resistance network in this version of the model is relatively simple as shown in Fig. 2 A. The total resistance, R, is divided into two major components, R_1 and R_M. The component R_1 consists of the boundary layer resistance and the stomatal resistance while R_M consists of all liquid phase resistances between the intercellular air spaces and the chloroplasts. The total resistance is affected by any factor which changes any of its components. Boundary layer resistance changes with wind speed, leaf size and leaf orientation (Vogel, 1970; Parkhurst et al., 1968; Raschke, 1956; Bange, 1953) and is taken as the boundary layer resistance to water vapor as shown in Eq. (16) multiplied by 1.56, the ratio of the diffusion coefficients for H_2O and CO_2 in air at $0°$ C.
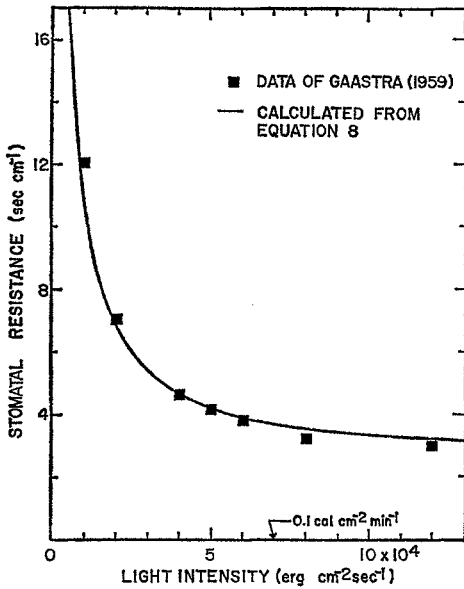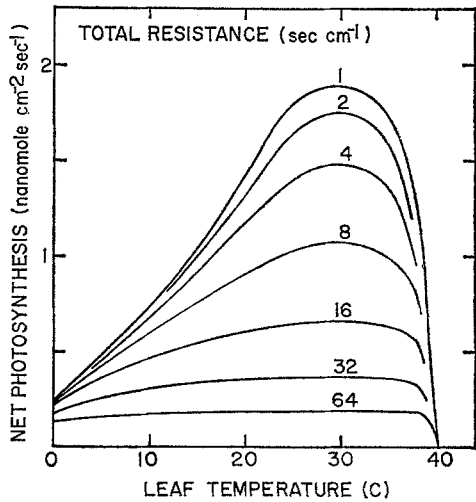
Fig. 3

Fig. 4

Fig. 3. Stomatal resistance as a function of light intensity (400–700 nm). The data points were taken from Table 11 of Gaastra (1959) for turnip in 0.03% CO_2 and air temperature 20.3° C. The solid line was calculated from Eq. (8) with $K_{RL} = 3.5 \times 10^5$ erg cm^{-2} s^{-1} and $_{min}R_S = 2.5$ cm s^{-1}. All symbols are defined in Appendix A

Fig. 4. Photosynthesis as a function of leaf temperature for several values of total CO_2 diffusion resistance, R. The simplified model [Eq. (3)] was used with $C_A = 12.5$ nM cm^{-3} (air concentration), $L = 4 \times 10^5$ erg cm^{-2} s^{-1} (full sun), $K = 10$ nM cm^{-3}, $T = 30°$ C (optimum), and values of other parameters as listed in Appendix A. All symbols are defined in Appendix A. (5 nM cm^{-2} s$^{-1} = 79$ mg dm^{-2} hr^{-1})

Stomatal resistance, R_S, is also known to change (Meidner and Mansfield, 1968; Zelitch, 1969). It changes with L, leaf water potential, the phase of the endogenous rhythm, T, and [CO_2]. In the absence of water stress, light intensity is probably the single most important factor determining stomatal aperture. Following Waggoner (1969) we use an inverted M-M type equation:

$$R_S = \frac{L + K_{RL}}{L} {}_{min}R_S \qquad (8)$$

where: $_{min}R_S$ is the minimum value of R_S reached at high light intensities (cm s^{-1})

K_{RL} is the value of L such that $R_S = 2({}_{min}R_S)$ (erg cm^{-2} s^{-1}).

Eq. (8) is graphed in Fig. 3 along with values of R_S observed in turnip (Gaastra, 1959). Leaf water potential is a function of several environmental factors and is very difficult to predict. The phase of the endogenous rhythm of most plants favors under natural conditions stomatal opening during the daylight hours. In the illustrations we have assumed that both the water potential and the endogenous rhythm favor full stomatal opening. Reports on the effect of temperature on steady-state stomatal apertures are contradictory (Meidner and Mansfield, 1968). However, in some species at least, *e.g. Zea mays*, stomatal diffusion resistance is significantly affected by temperature (Raschke, 1970). The nature of the effect of [CO_2] on stomatal apertures is unclear (Meidner and Mansfield, 1968; Zelitch, 1969). However, there is considerable evidence that at relatively low CO_2 levels the stomatal aperture increases with decreasing [CO_2] (Meidner and Mansfield, 1968). For simplicity no [CO_2] and T dependencies of R_S have been included in the illustrations at this time since the quatitative nature of these relationships is still relatively unclear.

As more information becomes available many of the estimates made in the above two paragraphs concerning the effects of environmental conditions on P_M, K and R can be refined and additional terms, *e.g.* [CO_2] and T dependencies of R_S, can be put into the model in order to more accurately describe photosynthesis.

To illustrate what has been discussed so far, photosynthesis as a function of several variables is shown in Figs. 4, 5, and 6. In Fig. 4, the variation of photosynthesis with T is shown for several values of R. It is evident that when the resistance is high, photosynthesis depends almost entirely on the rate of diffusion and is nearly independent of temperature, as predicted by Eq. (4).

In Fig. 5, the effect of changing K is shown on a plot of P versus C_A. Fig. 6 is similar to Fig. 5 except that R is changing instead of K. In both cases when $\dfrac{R P_M}{K} \gg 1$ a Blackman (1911) curve is approached, and when $\dfrac{R P_M}{K} \ll 1$ a Michaelis-Menten curve is approached. Blackman curves, which are characterized by two linear portions connected by a sharp elbow, result when the resistance to CO_2 uptake controls the rate of photosynthesis. Resistance is controlling when K is very small or R is large. Michaelis-Menten curves result when biochemical reactions control the rate of photosynthesis. This occurs either at large K or very small R.

B. Standard Version for Leaves which Respire in Light

Since most and possibly all plants respire in light it is necessary to add respiration to the simple model presented in Section A. Fig. 2
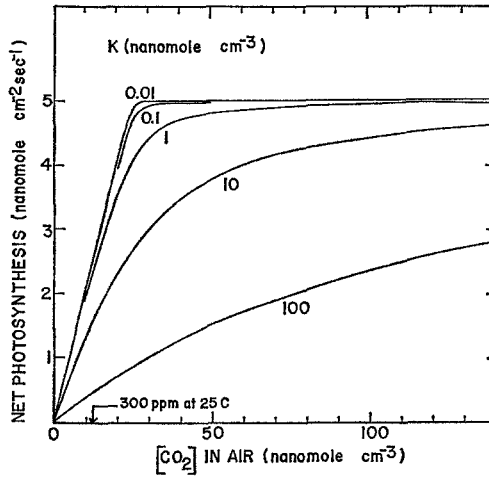
Fig. 5. Photosynthesis as a function of the CO_2 concentration in the air for several values of the Michaelis constant, K. The simplified model [Eq. (3)] was used with $R = 5$ s cm^{-1}, $T = 30°$ C (optimum), $L = 4 \times 10^5$ erg cm^{-2} s^{-1} (full sun), and values of other parameters as listed in Appendix A. All symbols are defined in Appendix A
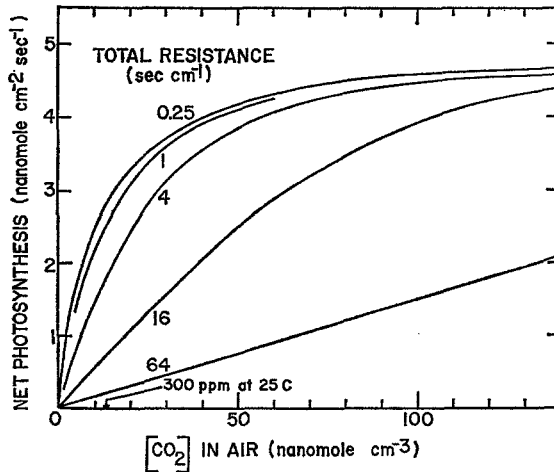

Fig. 6. Photosynthesis as a function of CO_2 concentration in the air for several values of total CO_2 diffusion resistance, R. The simplified model [Eq. (3)] was used with $K = 10$ nM cm^{-3}, $T = 30°$ C (optimum), $L = 4 \times 10^5$ erg cm^{-2} s^{-1} (full sun), and values of other parameters as listed in Appendix A. All symbols are defined in Appendix A

compares diagramatically the version of the model presented in Section A with the one we will now describe. Two differences are apparent: 1) a flux of CO_2 produced by respiration, W, is included, and 2) the resistance network (from Lake, 1967) is necessarily more complex.

Resistance R_1 is the resistance between the outside air and the intercellular air spaces (IAS), and is comprised of boundary layer and stomatal resistances. The $[CO_2]$ is assumed to be uniform throughout the IAS. Resistances R_2 and R_3 are the direct resistances between the IAS and the sites of photosynthesis and respiration, respectively, and both presumably contain cell wall and cytoplasm path-resistances. Finally, R_4 is the direct resistance between the sites of respiration and the chloroplasts. The indirect diffusion paths from the IAS to the chloroplasts are represented by $R_3 + R_4$. Thus, the net diffusive resistance "seen" by a CO_2 molecule between the IAS and the chloroplasts is R_2 in parallel with $(R_3 + R_4)$. Similar situations exist for the total resistances between the IAS and the sites of respiration, and between the sites of respiration and the chloroplasts. This triangle of resistances may seem to present more complications than necessary. This is discussed later. Compared with any real leaf, however, it is a great simplification. Also, to describe paths as direct or indirect is not completely satisfactory but is not avoidable in an electrical analogue with discrete circuit elements.

Proceeding as before we derive an exact expression for net photosynthesis as a function of P_M, K, the R's, W and C_A:

P_l = net photosynthesis

$$= \frac{[C_A + K + S_1(P_M - W) - WS_2] - \{[C_A + K + S_1(P_M - W) - WS_2]^2}{2S_1} \tag{9}$$

$$\frac{- 4S_1[(C_A - WS_2)(P_M - W) - WK]\}^{\frac{1}{2}}}{2S_1}$$

where the only new symbols introduced are S_1 and S_2, both having units of resistance:

$$S_1 \equiv R_1 + \frac{R_2(R_3 + R_4)}{R_2 + R_3 + R_4}, \tag{10}$$

$$S_2 \equiv \frac{R_2 R_4}{R_2 + R_3 + R_4}. \tag{11}$$

Mathematical details are given in Appendix C. Also in Appendix C are expressions for the $[CO_2]$ at the three resistance junctions inside the leaf. Environmental factors affecting K and R_1 were discussed in Section A.

Respiratory CO_2 produced in photosynthetic tissue during illumination has several sources. Following the terminology of Jackson and

Volk (1970), we use "mitochondrial respiration" (W_M) to refer to the sum of the classical dark respiratory pathways and "peroxisomal respiration" (W_P) to refer to the sum of the light-induced pathways the bulk of which involves glycolate metabolism. Consequently, $W = W_M + W_P$.

Mitochondrial respiration is probably almost completely suppressed in the light except at low light intensities (Hew et al., 1969; Forrester et al., 1966; Hoch et al., 1963; Irvine, 1970; Holmgren and Jarvis, 1967). Irvine (1970) measured the rate of respiration at various light intensities in sugar cane, a low compensation species, with an isotope method using a labeling sequence capable of measuring most of W_M but little if any W_P. Measured respiration declined sharply with increasing light intensity until it reached a very low rate at light intensities greater than one-fourth of full sunlight. This relationship, as approximated by the exponential component of Eq. (12), is used to describe the dependence of W_M on light intensity. The temperature dependence of W_M, $F(T)$, is well known. That used, is shown in Fig. 1. It is taken from the data of Rastorfer and Higinbotham (1968) for the same moss used for $G(T)$ for $T = 4$–$39°$ C and is estimated for $T < 4°$ C and $T > 39°$ C. Mitochondrial respiration is independent of C_A and C_{OA} (the O_2 concentration in the air expressed as a fraction (V/V), Forrester et al., 1966); hence no C_A and no C_{OA} dependence is included in the description of W_M. Thus

$$W_M = W_{MLT} \left\{ \exp \left[(-\ln 2) \left(\frac{L}{L_H} \right) \right] \right\} F(T) \qquad (12)$$

where: W_{MLT} (nM cm^{-2} s^{-1}) is the value of W_M at zero L and optimum T (45° C)

$\quad L_H$ (erg cm^{-2} s^{-1}) $\quad$ is a constant such that when $L = L_H$,

$$\exp \left[(-\ln 2) \left(\frac{L}{L_H} \right) \right] = 1/2$$

$\quad F(T)$ $\qquad\qquad$ is a temperature dependence of W_M.

There is doubt about the extent of W_P since its precise value is impossible to determine with the existing indirect methods of measurement (Jackson and Volk, 1970). However, it can be shown that W_P increases with increasing light intensity (Jackson and Volk, 1970; Holmgren and Jarvis, 1967; Hew et al., 1969; Decker, 1959), that its temperature dependence probably follows that of photosynthesis (Hofstra and Hesketh, 1969), except possibly at temperatures greater than the photosynthetic optimum (Jackson and Volk, 1970), that it increases with increasing C_{OA} (Forrester et al., 1966; Tregunna et al., 1966; Fock and Egle, 1966; Jackson and Volk, 1970), and that the effect of C_{OA} is governed by an interaction between C_{OA} and C_A (Jackson and Volk, 1970; Fock and Egle, 1966; Ellyard and Gibbs, 1969). For purposes of

illustration the following light, temperature, and C_{OA} dependencies will be used. No C_A dependence is included. These dependencies can be refined and a C_A dependency added as more information becomes available. The light dependence is taken to have the familiar M-M form with K_{WPL}, the M-M constant for the reaction having about the same value as K_L, the M-M constant for the light dependence of P_M. The temperature dependence is taken to be proportional to $G(T)$ (Fig. 1). The C_{OA} dependence is taken to increase linearly with C_{OA} since the CO_2 compensation concentration (Γ) is linearly dependent on C_{OA} (Forrester *et al.*, 1966). Thus

$$W_P = \frac{W_{PLTO} \, C_{OA} \, G(T)}{1 + \frac{K_{WPL}}{L}} \tag{13}$$

where W_{PLTO} (nM cm^{-2} s^{-1}) is the value of W_P at saturating L, optimum T, and $C_{OA} = 1.0$.

Oxygen probably influences photosynthesis in a variety of ways (Turner and Brittain, 1962). In addition to its previously mentioned effect on W_P, it may also have a variety of effects on the dark and light reactions of photosynthesis. O_2 competitively inhibits ribulose-diphosphate carboxylase with respect to CO_2 (Bowes and Ogren, 1970). The relative importance of this effect is not known and consequently no description is included in the model at this time. It is likely that C_{OA} also influences P_M. As C_{OA} increases P_M probably decreases since significant amounts of Calvin-cycle compounds appear to be shunted into the glycolate pathway at high C_{OA} (Ellyard and Gibbs, 1969) and the degree of inhibition of photosynthesis by O_2 at constant C_A and saturating L increases with increasing C_{OA} (Björkman, 1966). The form of the dependence of P_M on C_{OA} is not yet clear to us. For a convenient first approximation in the illustrations to follow we will assume a linear dependence such that if

$$\frac{(W_{PLTO}) \, C_{OA}}{P_{MLT}} = M \tag{14}$$

(M is dimensionless), then

$$P_M (L, T, C_{OA}) = [P_M (L, T)](1 - M). \tag{15}$$

O_2 may have additional effects on photosynthesis. These can be included in the model as their nature becomes clearer.

To illustrate this photosynthesis model for photorespiring plants (C_3 or high-compensation plants), Figs. 7 through 9 are given. Fig. 7 shows P_1, net photosynthesis, versus P_A for 5 different values of C_{OA}. The inhibition of net photosynthesis with increasing C_{OA} is clearly shown in this figure. The reasons are twofold (and nearly impossible to
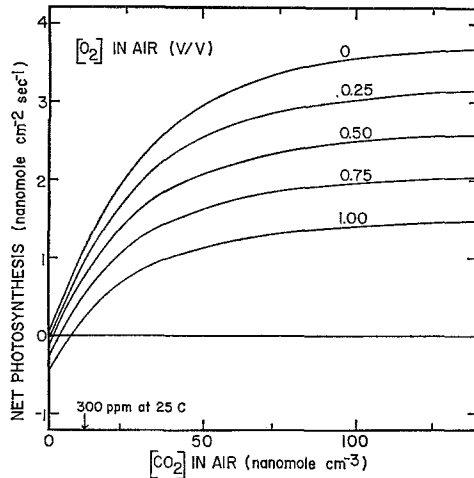
Fig. 7. Net photosynthesis as a function of CO_2 concentration in the air for several values of O_2 concentration in the air. The standard model [Eq. (9)] was used with values in Appendix A

separate from each other in the figure): 1) increased recycling of CO_2 inside the leaf due to the increase of W with increasing C_{OA} causes less CO_2 to be taken from the air, and 2) decreased P_M with increased C_{OA} invariably causes a decrease in gross photosynthesis and, consequently, net photosynthesis. Note that Γ increases with increasing C_{OA}. Increasing Γ with increasing C_{OA} has also been observed experimentally (Forrester *et al.*, 1966).

Fig. 8 shows P_1 versus L. Note that the light compensation-point decreases with increasing C_A as has been observed experimentally (Heath, 1969). The final example here, Fig. 9, shows P_1 versus C_A and C_C versus C_A for several values of K. The effect of respiration on the P_1 versus C_A curves is shown by comparing Figs. 9A and 5. Note that the curves resemble each other closely but that respiration lowers the maximum rates of net photosynthesis and results in negative net photosynthesis at low C_A. It is often assumed that $C_C \cong 0$ under optimum conditions of light and temperature, but Fig. 9B shows this is a reasonable assumption only when $C_A < R\,P_M$ and $\dfrac{R\,P_M}{K} \gg 1$. Note that in Blackman curves $C_A = R\,P_M$ at the elbow.

It is now appropriate to make a few additional comments about this version of the model. First, the magnitude of W is difficult to measure because of recycling within the leaf. This is discussed in some
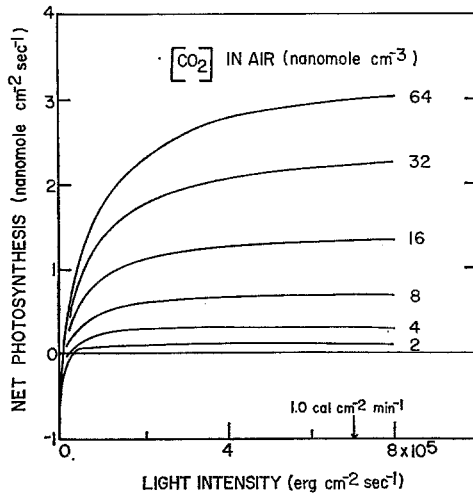
Fig. 8. Net photosynthesis as a function of light intensity for several values of CO_2 concentration in the air. The standard model [Eq. (9)] was used with values in Appendix A

detail by Samish and Koller (1968) and by Lake (1967) who give three methods (all of which can be shown to be mathematically and experimentally equivalent) of estimating W from the behavior of P_1 for C_A in the range 0 to Γ. This method is a distinct improvement over the earlier practice of estimating W by the value of net photosynthesis at zero C_A, but it assumes $[CO_2]$ at the chloroplasts is zero, which is equivalent to assuming $K = 0$, and it can easily be shown to give an underestimate of W which gets worse as K increases.

Samish and Koller (1968) raise two objections against Lake's model, which contains the same resistance network as ours, and which therefore deserve comment. First is the objection that we imply these resistances are separate and discrete. This is not the case, as seen earlier when we mention resistances represent "direct" or "indirect" paths and that the resulting complication is the penalty for including the possibilities we want and remaining with the electrical analogue. Second, the objection that we should not mathematically put three resistances where we cannot even measure one very well, is valid and can be answered only after a thorough experimental test of the model.

A reasonable assumption when testing this model is $R_2 = R_3$. Since the sites of both respiration and photosynthesis are located in the relatively thin layer of cytoplasm near the cell wall the diffusion paths represented by R_2 and R_3 are of similar length and $R_4 < R_2$ since R_4
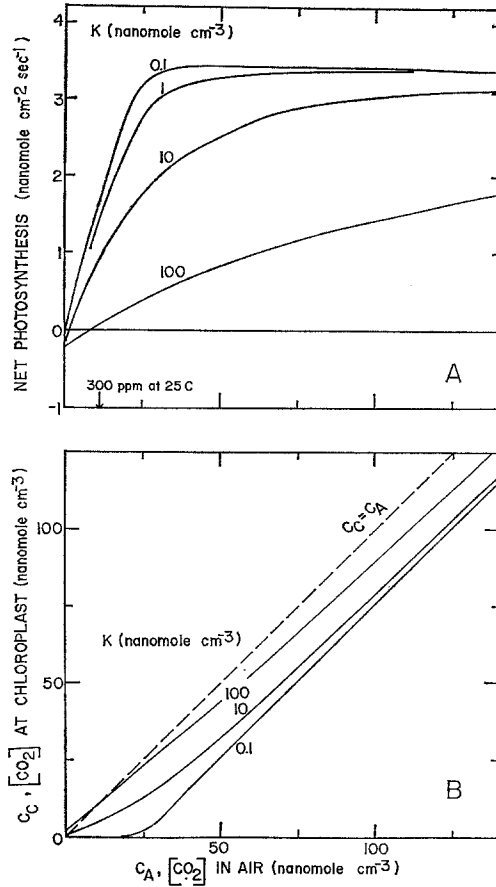
Fig. 9. A. Net photosynthesis as a function of CO_2 concentration in the air for several values of K. B. CO_2 concentration in the chloroplasts as a function of CO_2 concentration in the air for several values of K. The standard model [Eq. (9)] was used with values in Appendix A. All symbols are defined in Appendix A

does not contain a cell wall component and the chloroplasts and peroxisomes are often in close proximity (Frederick and Newcomb, 1969). (It was this reasoning which determined the choices of R_2, R_3 and R_4 in the examples illustrated.) The triangle of resistances formed by R_2, R_3 and R_4 may not cause as much complication as appears at first glance and may provide considerable latitude for interpreting photosynthesis data. Consider, for example, Samish and Koller's (1968) calculated values of r_p (their notation) a resistance which closely corresponds to R_2 in parallel with $(R_3 + R_4)$, hereafter $R_2 // (R_3 + R_4)$. If,

as suggested above, $R_2 \cong R_3$ and $R_4 < R_2$ then $R_2 // (R_3 + R_4) \cong R_2 // R_3 \cong R_2/2$. Consequently, if $R_2 // (R_3 + R_4)$ can be measured then R_2 and R_3 can be closely approximated.

Combining the Photosynthesis Model with the Leaf Energy Budget

Environmental conditions affect photosynthesis not only directly as seen in the photosynthesis model but also indirectly through their effects on leaf temperature. Leaf temperature is determined by energy exchange between the leaf and its environment and depends on several properties of the leaf as well as environmental conditions. The leaf energy budget describes the relationships between leaf properties, environmental conditions, transpiration, and leaf temperature (Gates, 1968). It can be combined with the photosynthesis model to first calculate leaf temperature and transpiration and then photosynthesis (Gates et al., 1969). The combined models are useful in evaluating the effects of wind speed, air temperature, relative humidity, incident radiation, CO_2 concentration, and leaf properties on both transpiration and photosynthesis.

The energy budget concept is straightforward: for a leaf in steady-state conditions its temperature is such that energy gained by the leaf equals the energy lost. The energy budget of a single leaf is expressed as follows (Gates, 1968):

$$Q_{ABS} = \quad RAD \quad + \quad C \quad + \quad L_v E$$

or

$$Q_{ABS} = \varepsilon \sigma (T + 273)^4 + K_1 \left(\frac{V}{D}\right)^{\frac{1}{2}} (T - T_A) + L_v \frac{d(T) - \text{r.h.} \, d(T_A)}{r_s + K_2 \frac{B^{0.20} D^{0.35}}{V^{0.55}}} \qquad (16)$$

where: Q_{ABS} is the absorbed radiation (erg cm^{-2} s^{-1})

RAD is radiation emitted (erg cm^{-2} s^{-1})

C is convective heat transfer (erg cm^{-2} s^{-1})

L_v is the latent heat of vaporization of water (erg nM^{-1})

E is transpiration (nM cm^{-2} s^{-1})

ε is the emissivity ($= 0.95$)

σ is the Stefan-Boltzmann constant $= 5.67 \times 10^{-5}$ erg cm^{-2}s^{-1} °K^{-4} (T in °C $+ 273 = T$ in °K)

K_1 is an empirically determined convection coefficient and $= 1.13 \times 10^4$ for $B \ll D$ or $B = D \leq 5$ cm and $= 7.0 \times 10^3$ for $B \gg D$ or $B = D > 5$ cm

T_A is the air temperature (°C)

V is the wind speed (cm s^{-1})

D is the leaf dimension along wind flow (cm)

B is the leaf dimension perpendicular to wind flow (cm)

$d(T)$ and $d(T_A)$ are the saturation densities of water vapor at T and T_A respectively (nM cm^{-3})

r.h.   is the relative humidity expressed as a number between 0 and 1

r_s is the stomatal diffusion resistance to water vapor (s cm^{-1})

$K_2 \dfrac{B^{0.20}\,D^{0.35}}{V^{0.55}}$ is the boundary layer resistance to water vapor (s cm^{-1}) where K_2 is another empirically determined constant $= 1.56$ for $B \ll D$ or $B = D \leqq 5$ cm and 2.10 for $B \gg D$ or $B = D > 5$ cm.

The radiation absorbed by the leaf (Q_{ABS}) consists of both long- (> 4 μm) and short-(< 4 μm)wave radiation. It depends on the leaf area exposed, the spectral absorptivity of the leaf, and the incident flux. Thus

$$A\,Q_{ABS} = \alpha_S\,A_S\,I_S + \alpha_L\,A_L\,I_L \tag{17}$$

where α_S, the short-wave absorptivity, is taken as 0.50 (Gates, 1965); α_L, the long-wave absorptivity, is 0.95 (Gates and Tantraporn, 1952); A is the total surface area of the leaf; A_S and A_L are the areas exposed to short-wave incident flux, I_S, and long-wave incident flux, I_L, respectively. In the illustrations Q_{ABS} is calculated with the following simplifying assumptions: a) the leaf is horizontal and located at the top of the canopy in such a way that the upper surface "sees" only sky and the sun and the lower surface "sees" only leaves and stems in the canopy interior, b) the temperature of the canopy interior is T_A and its emissivity is 0.95, c) no solar radiation is reflected to either leaf surface, and d) the skies are clear. Under these conditions the entire upper surface receives both short- and long-wave radiation, while the entire lower surface receives only long-wave radiation. The short-wave radiation incident on the upper surface (I_S) is taken from pyranometer measurements; and the long-wave radiation incident on the upper and lower surfaces is calculated from T_A with Swinbank's (1963) formula and the Stefan-Boltzmann law, respectively. Hence

$$\begin{aligned} Q_{ABS} = \tfrac{1}{2}\{0.50\,(I_S) &+ 0.95\,[5.31 \times 10^{-10}\,(T_A + 273)^6] \\ &+ 0.95\,(T_A + 273)^4\}. \end{aligned} \tag{18}$$

Transpiration (E) and P_1 are obtained simultaneously as follows. The desired environmental conditions and plant parameters are entered into Eq. (16) which is solved for E and T. The leaf temperature (T) is then entered into the photosynthesis model along with L to obtain P_1. The light intensity (L) is taken as $0.45\,I_S$ (Anderson, 1967) for direct and scattered sunlight.
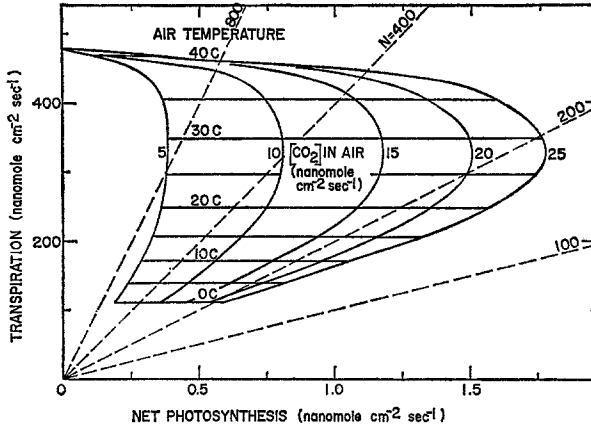
Fig. 10. Transpiration and net photosynthesis as functions of air temperature and CO_2 concentration in the air. The transpiration-assimilation ratio, N, is the number of molecules of H_2O transpired per molecule of CO_2 fixed. The energy budget [Eq. (16)] and the standard model [Eq. (9)] were used with values in Appendix A

Figs. 10–12 illustrate some of the descriptive and predictive capacity of the combined photosynthesis model and energy budget. They suggest the general nature of the various relationships and important areas of experimentation. The details of these figures and their interpretation are presented for illustration only. They are based on biological param-eters derived from several different plants. In addition some aspects of the photosynthesis model, e.g. environmental effects on stomatal aper-ture, may need further refinement after more experimental evidence is accumulated. Values of N, the transpiration-assimilation ratio, are indicated in Figs. 10 and 12 and plotted in Fig. 11 D. The transpiration-assimilation ratio is the number of H_2O molecules transpired per CO_2 molecule fixed and is an inefficiency index; plants with high N values use water less efficiently than plants with low N.

Fig. 10 shows that water-use efficiency improves with increasing C_A at constant T_A for all T_A in the case we have chosen. It also shows that for $C_A \gtrsim 12.5$ nM cm^{-3} (normal air concentration), N is almost independent of T_A between 0 and 15° C at constant C_A. At all other T_A and C_A, N increases with T_A at constant C_A. At $T_A \gtrsim 35°$ C, T is above optimum for photosynthesis and N increases rapidly with in-creasing T_A until it approaches infinity at $T_A \cong 40.7°$ C (the air tem-perature at which $T = 40°$ C and photosynthesis ceases). Finally, under the chosen conditions, the leaf uses water most efficiently at T_A between
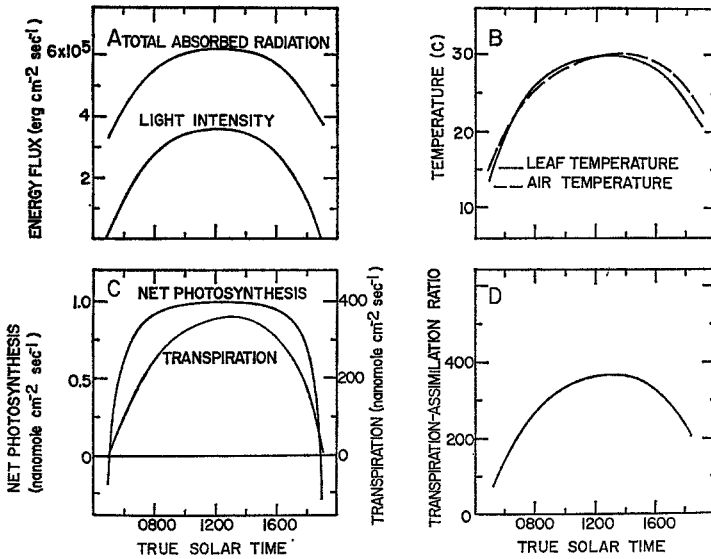
Fig. 11 A–D. Total absorbed radiation, light intensity, air temperature, leaf temperature, transpiration, net photosynthesis, and transpiration-assimilation ratio as a function of true solar time. Light intensity and air temperature in relation to true solar time are based on data in Fig. 78 of Geiger (1966) for a sunny day in mid-July in Palermo (38° 10′ N). Relative humidity was calculated with the assumption that absolute humidity was constant throughout the day and r.h. was 0.40 at maximum T_A. Eqs. (9), (16) and (18) were used with values in Appendix A to calculate the remaining curves

approximately 5 and 25° C and $C_A = 25$ nM cm^{-3} (approximately twice atmospheric concentration). Values for N vary from 155 to 170 in this regime.

Fig. 11 A–D shows L, Q_{ABS}, T_A, T, E, P_1 and N as functions of true solar time during the course of a hypothetical but typical day. Note that the net-photosynthesis curve (Fig. 11 C) rises steeply in the early morning to a broad plateau maintained during most of the day and then declines steeply in the late afternoon. All of the other curves rise and fall more slowly and have a much less distinct plateau. This indicates that the various factors governing photosynthesis interact to maintain photosynthesis at a relatively high and unchanging level throughout most of the day even though the individual factors governing it change considerably. Water-use efficiency (Fig. 11 D) is highest during the early morning and the late afternoon, while it is lowest in the early afternoon when T is highest. Values of N obtained around sunrise and sunset have been omitted. When P_1 passes through $P_1 = 0$ very large positive
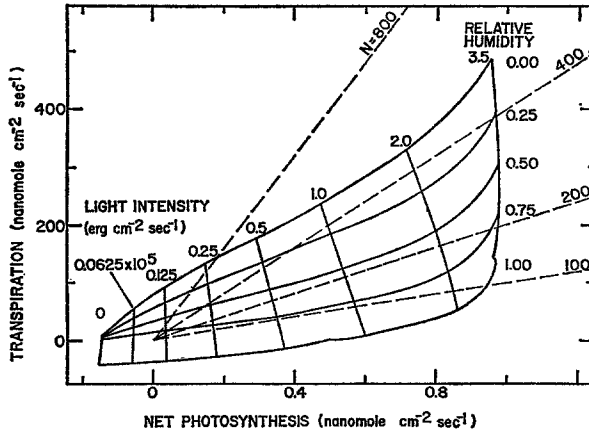
Fig. 12. Transpiration and net photosynthesis as functions of relative humidity and light intensity. Light intensity and T_A were taken from the morning hours in Fig. 11 A and B. Eqs. (9) and (16) were used with values in Appendix A

and negative values of N result which are mathematically correct but physiologically meaningless.

Fig. 12 shows a grid of r.h. versus L superimposed on E versus P_1 axes. In most of the central area of the grid, L has relatively little effect on water-use efficiency at constant r.h. In this region, i.e. between $L = 0.5$ and 2.0×10^5 erg cm^{-2} s^{-1} and r.h. between 0 and 0.75, increasing L by 400% changes N by no more than 35% along lines of constant r.h. At high $L (\gtrsim 3 \times 10^5$ erg cm^{-2} s^{-1}), N rises rapidly with increasing L. If values at still higher L were plotted the whole grid would fold back toward the left, as the r.h. $= 1.0$ line has already started to do, with the constant humidity lines pointing toward the upper left hand portion of the figure. At these L values, T exceeds the optimum for photosynthesis, and consequently P_1 decreases while E continues to increase producing ever larger N. Negative E indicates that water vapor is condensing on the leaf. The boundary layer resistance is the only resistance to water vapor diffusion for negative E since water condenses primarily on the outside of the leaf. Thus for negative E the stomatal resistance to water vapor diffusion, r_s, is deleted from Eq. (16). Negative E results in negative N if P_1 is positive. This occurs in Fig. 12 at r.h. $\cong 1.0$ and $L = 0.1$ to 0.75×10^5 erg cm^{-2} s^{-1}. In this case, negative N indicates extreme water-use efficiency. Note the discontinuity in the slope of the r.h. $= 1.0$ line at $E = 0$. At this point, condensation is replaced by transpiration and the diffusion resistance to water vapor changes abruptly.

15*

Appendix A

Symbols, Definitions, Units, and Typical Values Used in all Calculations Unless Specified Otherwise in the Figure Captions

Symbol	Definition	Typical Value	Units
A	Total surface area of leaf		cm^2
A_L	Area exposed to long-wave incident flux		cm^2
A_S	Area exposed to short-wave incident flux		cm^2
α_L	Long-wave absorptivity	0.95	
α_S	Short-wave absorptivity	0.50	
B	Dimension of the leaf perpendicular to wind flow	5	cm
C	Convective heat transfer		$erg\ cm^{-2}\ s^{-1}$
C_A	CO_2 concentration in the free air	12.5 at 25° C	$nM\ cm^{-3}$
C_C	CO_2 concentration in the chloroplasts		$nM\ cm^{-3}$
C_I	CO_2 concentration in the IAS		$nM\ cm^{-3}$
C_W	CO_2 concentration at the sites of respiration		$nM\ cm^{-3}$
C_{OA}	O_2 concentration in the air as a fraction (V/V)	0.25	
D	Dimension of the leaf along the wind flow	5	cm
$d(T), d(T_A)$	Saturation density of water vapor at T and T_A, respectively		$nM\ cm^{-3}$
E	Transpiration rate		$nM\ cm^{-2}\ s^{-1}$
ε	Emissivity	0.95	
$F(T)$	F as a function of T, a temperature dependence of W_M		
$G(T)$	G as a function of T, a temperature dependence of P_M and K_L		
Γ	CO_2 compensation concentration		$nM\ cm^{-3}$
IAS	Intercellular air spaces		
I_S	Short-wave incident flux ($\lambda < 4\ \mu m$)		$erg\ cm^{-2}\ s^{-1}$
K	A constant equal to C_C at which $P = P_M/2$	10	$nM\ cm^{-3}$
K_1	An empirically determined convection coefficient	see text	
K_2	An empirically determined constant	see text	
K_L	L at which $P_M(L) = P_{ML}/2$	1×10^5	$erg\ cm^{-2}\ s^{-1}$
K_{RL}	Value of L at which $R_S = 2\,(_{min}R_S)$	3.5×10^4	$erg\ cm^{-2}\ s^{-1}$
K_{WPL}	The M-M constant for the L dependence of W_P numerically the same as K_L	1×10^5	$erg\ cm^{-2}\ s^{-1}$
L	Light intensity (400–700 nm)	4×10^5	$erg\ cm^{-2}\ s^{-1}$
L_H	A constant such that when $L = L_H$, $\exp\left[(-\ln 2)\left(\dfrac{L}{L_H}\right)\right] = \dfrac{1}{2}$	1×10^4	$erg\ cm^{-2}\ s^{-1}$
L_v	Latent heat of vaporization		$erg\ nM^{-1}$

Symbol	Definition	Typical Value	Units
N	Number of water molecules transpired per CO_2 molecule fixed		
M	$= \dfrac{(W_{PLTO})\, C_{OA}}{P_{MLT}}$	0.29 at $C_{OA}=1$	
M-M	Michaelis-Menten		
Q_{ABS}	Absorbed radiation		erg cm^{-2} s^{-1}
P	Gross photosynthesis		nM cm^{-2} s^{-1}
P_1	Net photosynthesis (CO_2 flux through R_1)		nM cm^{-2} s^{-1}
P_2, P_3, P_4	CO_2 flux through R_2, R_3, and R_4 respectively		nM cm^{-2} s^{-1}
P_5	Gross photosynthesis (rate of CO_2 fixation in the chloroplasts)		nM cm^{-2} s^{-1}
P_M	Gross photosynthesis at saturating C_C for given L and T		nM cm^{-2} s^{-1}
P_{ML}	Gross photosynthesis at saturating C_C and saturating L for given T		nM cm^{-2} s^{-1}
P_{MLT}	Gross photosynthesis at saturating C_C, saturating L and optimum T	5	nM cm^{-2} s^{-1}
RAD	Radiation emitted		erg cm^{-2} s^{-1}
R	Total resistance to CO_2 diffusion		s cm^{-1}
R_M	Sum of all liquid phase resistances between the IAS and the chloroplasts		s cm^{-1}
R_S	Stomatal resistance to CO_2		s cm^{-1}
$\min R_S$	Minimum value of R_S reached at large L	2.5	s cm^{-1}
R_1	Boundary layer resistance plus stomatal resistance to CO_2 difussion	$1.65 + R_S$	s cm^{-1}
R_2	Direct resistance to CO_2 diffusion between the IAS and the sites of photosynthesis	5	s cm^{-1}
R_3	Direct resistance to CO_2 diffusion between the IAS and the sites of respiration	5	s cm^{-1}
R_4	Direct resistance to CO_2 diffusion between the sites of photosynthesis and respiration	1	s cm^{-1}
r_s	Stomatal diffusion resistance to water vapor		s cm^{-1}
r.h.	Relative humidity as a number between 0 and 1	0.5	
σ	Stefan-Boltzmann constant	5.67×10^{-5}	erg cm^{-2} s^{-1} $^\circ$K^{-4}
T	Leaf temperature	30	$^\circ$C
T_A	Air temperature		$^\circ$C
V	Wind speed	10	cm s^{-1}
W	Respiration		nM cm^{-2} s^{-1}
W_M	"Mitochondrial respiration", the sum of the classical dark respiratory pathways		nM cm^{-2} s^{-1}
W_{MLT}	W_M at zero L and optimum T (45° C)	1.2	nM cm^{-2} s^{-1}
W_P	"Peroxisomal respiration", the sum of the light induced respiratory pathways		nM cm^{-2} s^{-1}
W_{PLTO}	Value of W_P at saturating L, optimum T, and $C_{OA}=1.0$	1.45	nM cm^{-2} s^{-1}

Appendix B

Derivation of Eq. (3), Photosynthesis for a Plant without Respiration

Solve Eq. (1) for C_C and substitute into Eq. (2):

$$P = \frac{P_M}{1 + \dfrac{K}{C_A - RP}}. \tag{B.1}$$

Rearrange (B.1) to eliminate all fractions and put all terms on one side of the equation:

$$RP^2 - (C_A + K + R\,P_M)\,P + C_A\,P_M = 0. \tag{B.2}$$

This is now a quadratic in P of the familiar form

$$a\,x^2 + b\,x + c = 0$$

the solutions of which are:

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}.$$

Thus (B.2) has two solutions:

$$P = \frac{(C_A + K + RP_M) \pm [(C_A + K + RP_M)^2 - 4\,C_A\,R\,P_M]^{\frac{1}{2}}}{2R}. \tag{B.3}$$

To determine which solution is valid, we need to know that $P \to P_M$ as $C_A \to \infty$. For convenience in the following manipulations let the second term in the numerator of (B.3) be Z; i.e.

$$Z = [(C_A + K + R\,P_M)^2 - 4C_A\,R\,P_M]^{\frac{1}{2}}. \tag{B.4}$$

Factor out $(C_A + K + R\,P_M)^2$:

$$Z = (C_A + K + R\,P_M)\left[1 - \frac{4C_A\,RP_M}{(C_A + K + RP_M)^2}\right]^{\frac{1}{2}} \tag{B.5}$$

Expand using the binomial theorem:

$$Z = (C_A + K + R\,P_M)\left\{1 - \frac{1}{2}\,\frac{4C_A\,RP_M}{(C_A + K + RP_M)^2} + \frac{\frac{1}{2}(\frac{1}{2}-1)}{2!}\right.$$
$$\left.\left[\frac{-4\,C_A\,RP_M}{(C_A + K + RP_M)^2}\right]^2 + \cdots\right\}. \tag{B.6}$$

If $C_A \gg K$ and $C_A \gg R\,P_M$ then $\dfrac{C_A\,RP_M}{(C_A + K + RP_M)^2} \ll 1$ and successive terms in (B.6) will be smaller and smaller. For large enough C_A, Z is quite well approximated by

$$Z \cong (C_A + K + R\,P_M)\left(1 - \frac{1}{2}\,\frac{4\,C_A\,RP_M}{(C_A + K + RP_M)^2}\right). \tag{B.7}$$

Now substitude (B.7) into (B.3):

$$P \cong \frac{(C_A + K + RP_M) \pm (C_A + K + RP_M)\left[1 - \dfrac{4C_A\,RP_M}{2(C_A + K + RP_M)^2}\right]}{2R}.$$

Case I, taking $+$ sign, $P \cong \dfrac{2(C_A + K + RP_M) - \dfrac{2C_A\,RP_M}{(C_A + K + RP_M)}}{2R}$

$$\cong \frac{(C_A + K + RP_M)^2 - C_A RP_M}{R(C_A + K + RP_M)}$$

$$\lim_{C_A \to \infty} P = \frac{C_A^2 - 0}{RC_A} \to \frac{C_A}{R}.$$

Case II, taking $-$ sign,

$$P \cong \frac{2 C_A RP_M}{2 R(C_A + K + RP_M)}.$$

As $C_A \to \infty \quad \dfrac{C_A}{C_A + K + RP_M} \to 1 \quad$ so

$$\lim_{C_A \to \infty} P = \lim_{C_A \to \infty} \frac{P_M C_A}{C_A + K + RP_M} = P_M.$$

Thus the minus sign is what we want and

$$P = \frac{(C_A + K + RP_M) - [(C_A + K + RP_M)^2 - 4 C_A RP_M]^{\frac{1}{2}}}{2 R}$$

as in Eq. (3).

Appendix C

Derivation of Eq. (9), Net Photosynthesis as a Function of K, C_A, W, R_1, R_2, R_3, and R_4

A very important first assumption is that we have steady state conditions. Using the notation of Fig. 2, apply Fick's diffusion law across each of the four resistances:

$$P_1 = \frac{C_A - C_I}{R_1}, \tag{C.1}$$

$$P_2 = \frac{C_I - C_C}{R_2}, \tag{C.2}$$

$$P_3 = \frac{C_W - C_I}{R_3}, \tag{C.3}$$

$$P_4 = \frac{C_W - C_C}{R_4}. \tag{C.4}$$

Also, the flux of CO_2 diffusing away from any point in the circuit must equal the flux diffusing toward it. At the junction of resistances R_1, R_2, and R_3, we have

$$P_2 = P_1 + P_3. \tag{C.5}$$

Similarly,

$$W = P_3 + P_4, \tag{C.6}$$

$$P_5 = P_2 + P_4. \tag{C.7}$$

We now seek P_2, P_3, P_4 and P_5 in terms of P_1. If Eqs. (C.3) and (C.4) are rearranged:

$$C_W = C_I + P_3 R_3 \tag{C.8}$$

and

$$C_W = C_C + P_4 R_4. \tag{C.9}$$

Equate right hand sides of Eqs. (C.8) and (C.9):

$$C_I + P_3 R_3 = C_C + P_4 R_4. \tag{C.10}$$

If Eq. (C.2) is solved for C_C and Eq. (C.6) for P_4 and substituted into (C.10):

$$C_I + P_3\,R_3 = (C_I - P_2\,R_2) + (W - P_3)\,R_4 . \qquad (C.11)$$

Solve (C.5) for P_3, substitute into (C.11) and solve for P_2:

$$C_I + (P_2 - P_1)\,R_3 = C_I - P_2\,R_2 + (W - P_2 + P_1)\,R_4 , \qquad (C.12)$$

$$P_2 = \frac{P_1(R_3 + R_4) + W R_4}{R_2 + R_3 + R_4} , \qquad (C.13)$$

then,

$$P_3 = P_2 - P_1 = \frac{W R_4 - P_1\,R_2}{R_2 + R_3 + R_4} , \qquad (C.14)$$

$$P_4 = W - P_3\,\frac{W(R_2 + R_3) + P_1\,R_2}{R_2 + R_3 + R_4} \qquad (C.15)$$

and

$$P_5 = P_2 + P_4 = (P_1 + P_3) + (W - P_3) = P_1 + W . \qquad (C.16)$$

Thus, if we know P_1, W, R_1, R_2, R_3, and R_4 we can find P_2, P_3, P_4 and P_5 using (C.13) through (C.16). The concentrations, C_I, C_W and C_C can then be found by rearranging and combining (C.1), (C.2) and (C.3):

$$C_I = C_A - P_1\,R_1 , \qquad (C.17)$$

$$C_W = C_I + P_3\,R_3 = C_A - P_1\,R_1 + P_3\,R_3 \qquad (C.18)$$

and

$$C_C = C_I - P_2\,R_2 = C_A - P_1\,R_1 - P_2\,R_2 . \qquad (C.19)$$

We now wish to include the M-M equation:

$$P_5 = \frac{P_M}{1 + K/C_C} . \qquad (C.20)$$

First, substitute (C.13) into (C.19). After some rearrangement we get

$$C_C = C_A - P_1\,S_1 - W\,S_2 \qquad (C.21)$$

where

$$S_1 \equiv R_1 + \frac{R_2(R_3 + R_4)}{R_2 + R_3 + R_4} \qquad (C.22)$$

and

$$S_2 \equiv \frac{R_2 R_4}{R_2 + R_3 + R_4} . \qquad (C.23)$$

Second, substitute (C.16) and (C.21) into (C.20):

$$P_1 + W = \frac{P_M}{1 + \dfrac{K}{C_A - P_1\,S_1 - W\,S_2}} . \qquad (C.24)$$

Third, clear (C.24) of fractions:

$$S_1 P_1^2 - [C_A + K + S_1(P_M - W) - W S_2]$$
$$P_1 + (C_A - W S_2)(P_M - W) - W K = 0 . \qquad (C.25)$$

This equation, a quadratic equation in P_1, is now handled in the same way as Eq. (B.7) in Appendix B. The only difference is that

$$\lim_{C_A \to \infty} P_1 = P_M - W \qquad (C.26)$$

where without respiration we had

$$\lim_{C_A \to \infty} P = P_M . \qquad (C.27)$$

The minus sign in the solution of the quadratic is again the sign we want and we finally get:

$$P_1 = \frac{[C_A + K + S_1(P_M - W) - WS_2] - \{[C_A + K + S_1(P_M - W) - WS_2]^2}{2S_1}$$
$$\frac{-4S_1[(C_A - WS_2)(P_M - W) - WK]\}^{\frac{1}{2}}}{2S_1} \quad \text{(C.28)}$$

References

Anderson, M. C.: Photon flux, chlorophyll content, and photosynthesis under natural conditions. Ecology 48, 1050–1053 (1967).

Bange, G. G. T.: On the quantitative explanation of stomatal resistance. Acta botanica neerl. 2, 255–297 (1953).

Björkman, O.: The effect of oxygen concentration on photosynthesis in higher plants. Physiol. Plant. (Cph.) 19, 618–633 (1966).

Blackman, F. F., Smith, A. M.: Experimental researches on vegetable assimilation and respiration. IX. On assimilation in submerged water-plants and its relation to the concentration of carbon dioxide and other factors. Proc. roy. Soc. B 85, 389–412 (1911).

Bowes, G., Ogren, W. L.: The effect of light intensity and atmosphere on ribulose diphosphate carboxylase activity. Plant Physiol. 46, Suppl. 7 (1970).

Briggs, G. E., Haldane, J. B. S.: A note on the kinetics of enzyme action. Biochem. J. 19, 338–339 (1925).

Decker, J. P.: Comparative responses of carbon dioxide outburst and uptake in tobacco. Plant Physiol. 34, 100–102 (1959).

Ellyard, P. W., Gibbs, M.: Inhibition of photosynthesis by oxygen in isolated spinach chloroplasts. Plant Physiol. 44, 1115–1121 (1969).

Fock, H., Egle, K.: Über die „Lichtatmung" bei grünen Pflanzen. I. Die Wirkung von Sauerstoff und Kohlendioxyd auf den CO_2-Gaswechsel während der Licht- und Dunkelphase. Beitr. Biol. Pflanzen 42, 213–239 (1966).

Forrester, M. L., Krotkov, G., Nelson, C. D.: Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. I. Soybean. Plant Physiol. 41, 422–427 (1966).

Frederick, S. E., Newcomb, E. H.: Microbody-like organelles in leaf cells. Science 163, 1353–1355 (1969).

Gaastra, P.: Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. Meded. Landbouwhogeschool Wageningen 59, No. 11 (1959).

Gates, D. M.: Energy, plants and ecology. Ecology 46, 1–13 (1965).

— Transpiration and leaf temperature. Ann. Rev. Plant Physiol. 19, 211–238 (1968).

— Johnson, H. B., Yocum, C. S., Lommen, P. W.: Geophysical factors affecting plant productivity. Proc. Int. Symp. Productivity of Photosynthetic Systems. Pt. II: Theoretical foundations of optimization of the photosynthetic productivity. Moscow, U.S.S.R. Sept. 1969 (in press).

— Tantraporn, W.: The reflectivity of deciduous trees and herbaceous plants in the infrared to 25 μ. Science 115, 613–616 (1952).

Geiger, R.: The climate near the ground (transl. from German Scripta Technica, Inc.). Cambridge, Mass.: Harvard Univ. Press 1966.

Heath, O. V. S.: The physiological aspects of photosynthesis. Stanford, Calif.: Stanford University Press 1969.

Hew, Ch.-S., Krotkov, G., Canvin, D. T.: Determination of the rate of CO_2 evolution by green leaves in light. Plant Physiol. 44, 662–670 (1969).

Hoch, G., Owens, O. v. H., Kok, B.: Photosynthesis and respiration. Arch. Biochem. 101, 171–180 (1963).

Hofstra, G., Hesketh, T. D.: Effects of temperature on the gas exchange of leaves in the light and dark. Planta (Berl.) 85, 228–237 (1969).

Holmgren, P., Jarvis, P. G.: Carbon dioxide efflux from leaves in light and darkness. Physiol. Plant. (Cph.) 20, 1045–1051 (1967).

Honert, T. H. van den: Carbon dioxide assimilation and limiting factors. Rec. Trav. bot. néerl. 27, 149–284 (1930).

Irvine, J. E.: Evidence for photorespiration in tropical grasses. Physiol. Plant. (Cph.) 23, 607–612 (1970).

Jackson, W. A., Volk, R. J.: Photorespiration. Ann. Rev. Plant Physiol. 21, 385–432 (1970).

Lake, J. V.: Respiration of leaves during photosynthesis. I. Estimates from an electrical analogue. Aust. J. biol. Sci. 20, 487–493 (1967).

Meidner, H., Mansfield, T. A.: Physiology of stomata. Maidenhead, England: McGraw-Hill 1968.

Parkhurst, D. F., Duncan, P. R., Gates, D. M., Kreith, F.: Wind-tunnel modelling of convection of heat between air and broad leaves of plants. Agr. Meteorol. 5, 33–47 (1968).

Raschke, K.: Über die physikalischen Beziehungen zwischen Wärmeübergangszahl, Strahlungsaustausch, Temperatur und Transpiration eines Blattes. Planta (Berl.) 48, 200–238 (1956).

— Temperature dependence of CO_2 assimilation and stomatal aperture in leaf sections of Zea mays. Planta (Berl.) 91, 336–363 (1970).

Rastorfer, J. R., Higinbotham, N.: Rates of photosynthesis and respiration of the moss Bryum sandbergii as influenced by light intensity and temperature. Amer. J. Bot. 55, 1225–1229 (1968).

Saitoh, M., Narita, K., Isikawa, S.: Photosynthetic nature of some aquatic plants in relation to temperature. Bot. Mag. Tokyo 83, 10–12 (1970).

Samish, Y., Koller, D.: Photorespiration in green plants during photosynthesis estimated by use of isotopic CO_2. Plant Physiol. 43, 1129–1132 (1968).

Swinbank, W. C.: Long-wave radiation from clear skies. Quart. J. roy. Met. Soc. 89, 339–348 (1963).

Tregunna, E. B., Krotkov, G., Nelson, C. D.: Effect of oxygen on the rate of photorespiration in detached tobacco leaves. Physiol. Plant. (Cph.) 19, 723–733 (1966).

Turner, J. S., Brittain, E. G.: Oxygen as a factor in photosynthesis. Biol. Rev. 37, 130–170 (1962).

Vogel, S.: Convective cooling at low airspeeds and the shapes of broad leaves. J. exp. Bot. 21, 91–101 (1970).

Waggoner, P. E.: Predicting the effect upon net photosynthesis of changes in leaf metabolism and physics. Crop Sci. 9, 315–321 (1969).

Warburg, O.: Über die Geschwindigkeit der photochemischen Kohlensäurezersetzung in lebenden Zellen. Biochem. Z. 100, 230–270 (1919).

Zelitch, I.: Stomatal control. Ann. Rev. Plant Physiol. 20, 329–350 (1969).

P. W. Lommen
Missouri Botanical Garden
2315 Tower Grove Avenue
St. Louis, Missouri 63110, U.S.A.