Development of a Photosynthesis Model with an Emphasis on Ecological Applications

I. Theory

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Summary. In this paper, a description of photosynthesis in a single leaf is developed that separates physiological sub-processes and that is practical to apply as an ecological tool. Temperature dependencies are emphasized with the ultimate aim of linking such a description of photosynthesis with equations describing the energy budget of particular leaves. The description of photosynthesis can be applied to C_4 plants at this time and is needed to describe photosynthesis in C_3 plants when photorespiration is included. If the model is used to analyze at various times the response of a plant adjusting its metabolism to changes in light, temperature, or other factors experienced during growth, we will obtain a dynamic picture of the acclimation process. It will also be possible to determine the phenotypic plasticity of particular plants with respect to the metabolic sub-processes outlined.

Introduction

The behavior and changes in behavior observed in an organism responding to the natural environment can clarify the means by which specific organisms survive in particular environments. Survival and success of an organism occurs when the individual manages to correctly respond to information it senses about the environment. To assess the response of plants to environmental factors, fairly elaborate tools are needed because much of plant behavior takes place at the biochemical and cellular level. These tools involve conceptual formulations as well as actual instrumentation. Limitations in our understanding can result from inadequacy in either.

The interrelationship of transpiration and leaf temperatures for example was of interest to investigators for 75 years before it was well understood. Raschke (1956, 1960) and Gates (1963, 1968) clarified this by bringing to a focus the importance of understanding plant environment interactions with the energy budget concept. Since photosynthesis, as well as transpiration, is temperature dependent, the concept of energy budget is one of our most significant analytical tools for understanding plant behavior.

In 1971, Lommen et al. proposed an analytical model to describe the interaction of biological and environmetal factors governing the gas diffusion and biochemical processes of photosynthetic carbon dioxide fixation in a single leaf. This analytical model is a second suggested conceptual tool allowing investigation, and most importantly, *integration* of aspects of plant behavior closely linked to survival. This description combined with the leaf energy budget, allows simultaneous calculation of transpiration and photosynthesis rates for a given set of environmental conditions. If this steady-state model is applied to a leaf in its natural environment, one can examine a number of ecologically important relationships for a particular leaf by integrating the established steady-state rates over time. The amount of photosynthate accumulated, the amount of water used, and the efficiency of water utilization can be estimated for any time period.

Tool design must correspond to the intended application. Since the proposed analysis is intended primarily for ecological purposes, it must incorporate sensitivities of major sub-processes to environmental variables of major importance. In the context of the analysis proposed, the environmental components singled out as being of major importance are incident radiant flux, air temperature, wind speed, humidity, and gas composition of the atmosphere. From these one can determine further variables important to the leaf, i.e. gas composition in the intercellular air space and leaf temperature. Each of these environmental components may affect any or all of the sub-processes included in the photosynthesis model. To be of use ecologically, the model structure should allow separation of environmental effects on individual sub-processes such that a change in a sub-process with time (acclimation) can be determined and the significance of change with respect to survival can be assessed. The photosynthesis model structure given here differentiates the following sub-processes: regulation of leaf diffusion resistance by stomata, transport of carbon dioxide from the intercellular air space to the site of carbon dioxide fixation, enzymatic fixation of carbon dioxide, production of photoproducts in the light reactions, and reutilization of photosynthate in the simultaneous processes of dark respiration and photorespiration.

The research described in this and following publications is a further development of the Lommen et al. (1971) photosynthesis model. Development of the analysis is based on experimental results obtained by measuring photosynthetic responses in red kidney bean seedlings. Interpretation of the data and the approach taken to resolve conflicts between observed data and the model structure suggested by Lommen et al. (1971) reflect the desire to perfect a tool useful in investigating specific ecological problems. Such problems as light and temperature acclimation (see for example Mooney and Harrison, 1970) can best be investigated in the context of a framework such as that considered here.

Model Structure

1. General Considerations

Initial attempts at analyzing photosynthesis in plant leaves to a great extent led to empirical models. Chartier (1966) made the first steps toward reducing

empiricism by combining kinetic equations describing carbon metabolism with equations containing diffusion resistances to transport of carbon dioxide from source to sink (atmosphere to chloroplast). Such terms are included in the formulation described here.

Recent attempts in this field have been concerned mainly with description of photorespiration (Laisk, 1970; Hall, 1970; Hall and Björkman, 1975; Lommen et al., 1975; Peisker, 1974; Peisker and Apel, 1975). The hypothesis that has been made in these researches is that photorespiration is controlled by an oxygenase reaction performed by ribulose diphosphate carboxylase. Oxygen and carbon dioxide are thought to compete for the same enzyme-substrate complex (carboxylase plus ribulose diphosphate) and the reaction products are either 3-phosphoglycerate (carboxylation – photosynthesis) or 3-phosphoglycerate and phosphoglycolate (oxygenation – photorespiration). Phosphoglycolate is oxidized via the photorespiratory pathway. A number of biochemical studies support this hypothesis (Bowes et al., 1971; Berry, 1971; Bowes and Ogren, 1971; Bowes and Berry, 1972; Andrews et al., 1973; Lorimer et al., 1973). Recent evidence indicates that as carbon dioxide concentration decreases in the chloroplasts during photosynthesis, pH increases and oxygen inhibition of net photosynthesis becomes more prominent. Furthermore, a shift of products from photosynthetic to photorespiratory is seen (Robinson and Gibbs, 1975; Servaites and Ogren, 1975).

Net photosynthetic responses to oxygen and carbon dioxide concentration changes are consistent with formulations based on the competitive hypothesis (Björkman, 1971; Servaites and Ogren, 1975; Viil and Parnik, 1974; Lommen et al., 1975). Because we have chosen a different starting point, photorespiration is not described in this paper. It is however a sub-process identified in the formulation that can be investigated in subsequent stages. The above mentioned hypothesis can then be incorporated in explaining the net photosynthesis responses observed.

The description considered here is consistent with the philosophy developed in the modeling attempts mentioned. Major molecular constituents and reactions are separated as sub-processes that can be studied individually when considered in the proper order and under the proper conditions. It is felt that the *description undertaken here differs* from those mentioned above in that *temperature dependencies are emphasized* as the major consideration. *Emphasizing temperature* dependencies of all components and parameters *allows interfacing with equations describing the leaf energy budget* which is our most powerful tool for linking leaf and environment.

To serve a dual purpose (1. to elaborate a description applicable to C_4 plants and 2. to provide fundamental information about the C_3 photosynthetic system), our analysis has been developed from data obtained with bean seedlings where the first conditions under which photosynthesis is investigated are conditions of 1.5% oxygen and saturating carbon dioxide. These are unnatural conditions to the plant but are important because photorespiration is essentially zero at low pO_2 and the plant response of "total photosynthesis" can be studied with respect to light and temperature alone. These responses must subsequently be combined with carbon dioxide and oxygen effects to produce a model of the wide scope required in ecological studies. It is premature to compare the present results under these specialized conditions to field observations of photosynthesis

or to compare the model at this intermediate stage of development to other models.

In the experimental study of photosynthesis, incident light and leaf temperature are easily controlled. Oxygen concentration is readily held constant since it is present at a concentration large enough to be altered only slightly by the diffusion resistance of the leaf. Since photorespiration has a low affinity for oxygen (apparent $K_m \simeq 375\,\mu M$; Laing et al., 1974) and respiration has a high affinity (apparent $K_m \simeq 50\,nM$; Ikuma, H., unpublished), a concentration of oxygen was selected ($1.5\% \, O_2 \simeq 20\,\mu M$) which largely inhibits the former while not inhibiting the latter. Carbon dioxide concentration internal to the leaf (which the leaf cells see as an environmental variable) is impossible to hold constant during experimentation due to stomatal resistance changes. It was however determined for particular experiments. If other variables are to be studied as well, one should first define those that can be held constant. With these held constant (in the present research, light intensity and leaf temperature), one can study the response to experimentally determined values of the other variables (in this case carbon dioxide).

The following sequential consideration of variables was used to elaborate the model. First saturate photosynthesis with carbon dioxide and maintain a minimal oxygen concentration. Thus, photorespiration is turned off. A surface in three dimensions [discussed further in Eqs. (6) and (7) following] is determined for photosynthesis with respect to incident light and leaf temperature where photosynthesis is already maximized with respect to carbon dioxide and oxygen. This surface should on its initial slope reveal the maximum efficiency of light utilization for a particular plant and at the light maxima should reveal the temperature dependency at maximum of the over-all carbon fixation cycle. The surface should be valid for any combination of oxygen and carbon dioxide concentrations as a maximum surface if these two variables do in fact act in a competitive manner ,in photosynthesis and photorespiration. Photorespiration reduces photosynthesis by one third to one half but, even so, the maximum surface applies if the carbon dioxide concentration is increased sufficiently. In a subsequent step, carbon dioxide concentration can be reduced. Finally oxygen can be variably increased to include photorespiration.

2. Light Response Curves at Saturating CO_2 Concentration

In step one of the sequence outlined above, however, one discovers that a reasonable description of photosynthetic light response curves is difficult to formulate. Several processes may contribute to the over-all response. First, it is reasonable to postulate that the rate of photosynthesis depends on concentrations of photoproducts available (ATP or $NADPH_2$) and follows Michaelis-Menten kinetics. At low light intensity ATP or $NADPH_2$ are produced approximately as a linear function of light intensity (Black et al., 1962, 1963; Kahn, 1962; Krogmann, 1960; Sakurai et al., 1965; Shen and Shen, 1962) (ATP production may also involve a lag at low light intensity) while at higher light intensities the rate levels off to some maximum value. The highest rates of electron transport (hence ATP or $NADPH_2$ production) that have been observed in isolated chloroplasts would

be adequate to support carbon dioxide fixation at a rate twice as high as has been observed for isolated ribulose diphosphate carboxylase (Gould and Izawa, 1973; C.F. Yocum, unpublished; Zelitch, 1971).

The rate of carbon dioxide fixation as a function of light intensity at saturating carbon dioxide concentration in a coupled system would depend on the steady-state concentrations of ATP established (or $NADPH_2$ — whichever is limiting; for simplicity ATP will be used here). *At low light intensities* these concentrations may *depend only on the rate of ATP formation* if carbon dioxide fixation can keep pace with the ATP generating process (has a low K_{ATP}). Then at low light:

$$v_1 \simeq m \cdot L \tag{1}$$

and

$$v_2 = \frac{R_{MCO_2}}{1 + \dfrac{K_{ATP}}{[ATP]}} \tag{2}$$

where: L is the incident photosynthetically active radiant flux (PhAR in μEinsteins $cm^{-2} s^{-1}$),

m is a constant relating rate of ATP formation to light intensity,

v_1 is the rate of ATP formation,

v_2 is the rate of ATP consumption in CO_2 fixation which is in turn dependent on ATP concentration,

R_{MCO_2} is the maximum rate of CO_2 fixation in the carbon cycle,

K_{ATP} is the ATP concentration necessary to attain a fixation rate equal to one half R_{MCO_2},

at steady-state:

$$\frac{dATP}{dt} = 0 = (v_1 - v_2) \quad \text{and} \quad v_1 = v_2 \tag{3}$$

where v_1 is only dependent on incident light intensity. As light intensity increases, however, the rate of fixation must approach R_{MCO_2} as a limit and ATP production must become dependent on recycling of photoproducts in a shuttle system. Therefore ATP production rate probably does not attain the maximum rate possible for that process.

These observations alone might account for the shape of the light response curve but they are difficult to elaborate further on the basis of present plant physiological knowledge. Experimental investigations that would clarify the relationships are difficult to formulate and would be a major undertaking. The possibility of an actual diffusion resistance for photoproduct involved in the shuttle to the carboxylation sites should not be ignored even though the sites of phosphorylation appear to be closely associated with carboxylation enzymes. Absorption of light along its path through the leaf or chloroplast can be substantial (Nobel, 1974) and may be an important factor in the observed over-all photosynthetic response as shown for a simple canopy model by Horn (1971) (see also Rabinowitch, 1951, for remarks on heterogeneity of the system).

From the above discussion, it is clear that the light response curve is difficult to formulate from basic theoretical considerations alone. Nevertheless, an

analytical description of the three dimensional surface with photosynthesis as a function of light intensity and leaf temperature is essential in the sequential development of an ecological model involving all of the environmental variables outlined above. An empirical function to describe the light response is presented in a following paper concerning analysis of data from *Phaseolus vulgaris*. For now, the following general equation suffices:

$$P_M = f(L, P_{ML}, \ldots) \tag{4}$$

where: P_M is the rate of photosynthesis at a *specific L*, saturating carbon dioxide, and a specific leaf temperature,

P_{ML} is the rate of photosynthesis at *saturating L*, saturating carbon dioxide, and a specific leaf temperature.

It is possible to distinguish the two components of the light response curve representing individual processes, i.e. a linear portion where ATP production may govern the over-all response and the plateau region where enzymes in the Calvin cycle may govern the response.

3. Residual Respiration

Any observable respiration (compensation points greater than zero light intensity or carbon dioxide concentration) will be considered as residual mitochondrial respiration. 1.5% oxygen still saturates that process. Respiration estimates (primarily at high temperatures) can be made by linear extrapolation of the photosynthesis versus light intensity curves below zero net photosynthesis. This residual respiration is expected to increase with increasing leaf temperature and should depend on the activation energy of the rate limiting enzymatic step in the over-all process. The rate as a function of temperature should conform to the following equation observed by Arrhenius (1915) to describe temperature activated enzymatic reactions.

$$W = J \cdot e^{\left[-\frac{E}{RT_K} + A\right]} \tag{5}$$

where: W is the rate of respiration (picomoles $cm^{-2} s^{-1}$),

J provides the proper units = 1 picomole $cm^{-2} s^{-1}$,

E is the apparent activation energy of the process (cal M^{-1}),

R is the gas constant (1.987 cal °Kelvin^{-1} M^{-1}),

T_K is the absolute leaf temperature (°Kelvin),

e^{-E/RT_K} is the Boltzmann factor ($n_{activated}/n_{total}$), the fraction of molecules possessing a certain energy necessary to react (M M^{-1}),

A is an empirically determined constant.

In all analyses in which response curves are analyzed in a following paper to obtain parameters, any observed residual respiration is first added to net photosynthesis. *Estimated total photosynthesis* is then treated as described above as a function of incident light.
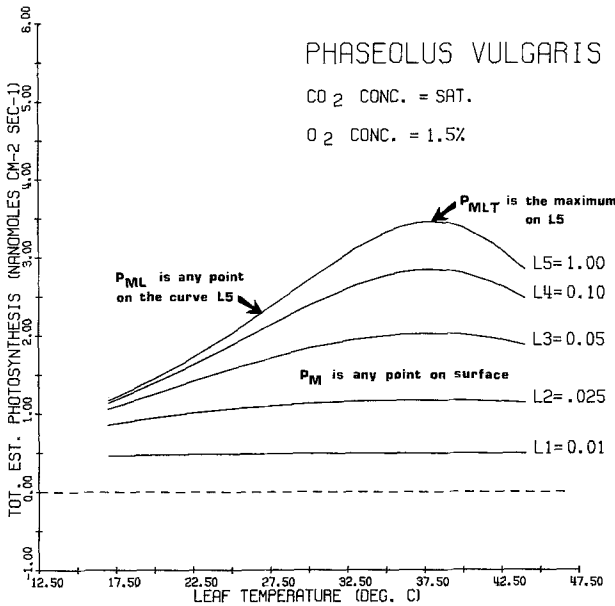
Fig. 1. Illustration of the P_M surface described in the text projected onto the total photosynthesis and leaf temperature plane. Solid lines are for equal photosynthetically active radiant flux (*PhAR*) as indicated in μEinsteins cm^{-2} s^{-1}. The relationship to each other of the several photosynthetic maxima P_{MLT}, P_{ML}, and P_M are shown

4. Leaf Temperature

The individually described analyses above are combined into a single scheme in the following manner. If carbon dioxide concentration is kept very high (approximately 1,500 ppm) in the atmosphere external to the leaf, a somewhat lower (due to boundary layer and stomatal resistances) but still saturating concentration of carbon dioxide for any incident light intensity is maintained at the cell walls internal to the leaf and at the chloroplasts. One must of course choose a plant that does not entirely close its stomata at high carbon dioxide concentration. Under these conditions a three dimensional surface (shown as determined for *Phaseolus vulgaris* in Fig. 1) describes the rate of photosynthesis as a function of incident light and leaf temperature where:
with $[O_2] = 1.5\%$,

$$P_{ML} = P_{MLT} \cdot G(T_K) \tag{6}$$

and

$$P_M = f(L, P_{ML}, \ldots). \tag{7}$$

where: P_{MLT} is the rate of photosynthesis at *saturating L, saturating* carbon dioxide, and *optimal* leaf temperature [nM cm^{-2} s^{-1}; see also Eq. (4)],
$G(T_K)$ is the temperature dependence (absolute scale) of P_{ML}/P_{MLT}.

If the simplest formulation holds, $G(T_K)$ should depend on the temperature of activation of the rate limiting enzymatic step of the process and on the temperature activation of the denaturation of the rate limiting enzyme at high temperatures. Johnson et al. (1942) have derived the following equation to explain the temperature response of a system where these two processes are the only processes involved. It has been shown to hold for many cases of the type described here (Koffler et al., 1947; Johnson et al., 1954).

$$I = \frac{C_2 \cdot T_K \cdot e^{-\Delta H \neq /R \cdot T_K}}{1 + e^{-\Delta H_1/R \cdot T_K} \cdot e^{\Delta S/R}} \tag{8}$$

where: I is the rate of photosynthesis at saturating carbon dioxide and saturating light and a particular leaf temperature; it is expressed as a decimal fraction of the rate at the optimal temperature (which we call $G(T_K)$) times 100, i.e. values will always be between 0 and 100,

C_2 is a constant (see Johnson et al., 1954),

$\Delta H \neq$ is the energy of activation for the enzyme catalyzed reaction (cal M^{-1}),

ΔH_1 is the energy of activation for the denaturation equilibrium (cal M^{-1}),

ΔS is the entropy of the denaturation equilibrium (entropy units).

For the system considered here, one should note:

$$G(T_K) = \frac{I}{100}. \tag{9}$$

Koffler et al. (1947) state that "the formulation applies to a given enzyme system, and it is precisely applicable, therefore, to a single system. It is approximately correct when the over-all effects occur in the manner of a series of a single system, as when one member of a series is largely limiting. In a complex process, the validity of the theory is tested by its conformity to the data". This conformity is evaluated in a following publication. Equation (8) could be used rather than the Arrhenius equation for residual respiration except that the temperature maximum for that process is very high, making it impossible to derive all of the parameter values.

All measured values of photosynthesis in light response curves are already maximum rates with respect to carbon dioxide. The following terminology outlined in Equations (4), (6), and (7) is therefore adopted (shown in Fig. 1). The maximum rate with 1.5% oxygen, optimal temperature, saturating carbon dioxide, and saturating light is designated as P_{MLT}. Any point on the $[G(T_K) \cdot P_{MLT}]$ curve is a maximum rate for 1.5% oxygen, saturating carbon dioxide, and saturating light at a specific leaf temperature and is designated a P_{ML} value. Any point on the P_M surface is a maximum rate for low oxygen and saturating carbon dioxide (light and leaf temperature specified) and is designated as P_M. P then refers to values obtained as carbon dioxide is decreased below saturating concentrations with light and leaf temperature fixed. With residual respiration corrected, the photosynthetic response with respect to carbon dioxide and 1.5% oxygen is formulated as follows.

5. Carbon Dioxide Response Curves

The physical process of carbon dioxide diffusing from the atmosphere (in the gas spaces internal to the leaf) to the site of carbon dioxide fixation in the chloroplast is described by Fick's law;

$$P = \frac{C_w - C_c}{R_M} \qquad (10)$$

where: P is the photosynthetic rate (nM cm^{-2} s^{-1}),
C_w is the carbon dioxide concentration in the intercellular air spaces of the leaf or at the cell walls of photosynthesizing leaf cells (nM cm^{-3}),
C_c is the carbon dioxide concentration in the chloroplasts (nM cm^{-3}),
R_M is the mesophyll resistance to carbon dioxide diffusion from the cell walls to the sites of fixation (s cm^{-1}).

Assuming further, as has commonly been the practice, that the over-all carbon fixation reaction follows Michaelis-Menten kinetics, then photosynthesis is also described by the following:

$$P = \frac{P_M}{1 + \dfrac{K_c}{C_c}} \qquad (11)$$

where: K_C is a constant equal to the chloroplast concentration of carbon dioxide at which $P = P_M/2$.

Solving Equation (10) for C_c, substituting into Equation (11), and solving the quadratic gives:

$$P = \frac{(C_w + K_C + R_M P_M) - [(C_w + K_C + R_M P_M)^2 - 4 C_w R_M P_M]^{\frac{1}{2}}}{2 R_M}. \qquad (12)$$

This resulting relationship is diagrammed in Figure 2 for any P_M point in the plane projection of Figure 1.

Jones and Slatyer (1972) have also interpreted the observed photosynthesic rates as a function of carbon dioxide concentration by including a transport resistance with the carboxylation reaction. Their arrangement of the quadratic provides a linear equation for the variables $C_w(P_M - P)/P$ and P by factoring out C_w. If P_M is known, R_M and K_C can be determined from the intercept and slope of the line obtained when ordered pairs of C_w and P are substituted to generate these new variables. A non-linear least squares solution considering original variables is preferable and allows P_M to be estimated by iteration which cannot be done with the formulation of Jones and Slatyer (1972).

Lommen et al. (1971) demonstrated that the over-all appearance of the response curve depends on the ratio $R_M P_M/K_C$. Most commonly observed photosynthetic responses tend toward so-called Blackman type response curves characterized by two linear portions connected by a fairly sharp elbow. This is produced from the quadratic when R_M is large or K_C is small and resistance dominates the response, i.e. $R_M P_M/K_C \gg 1$.
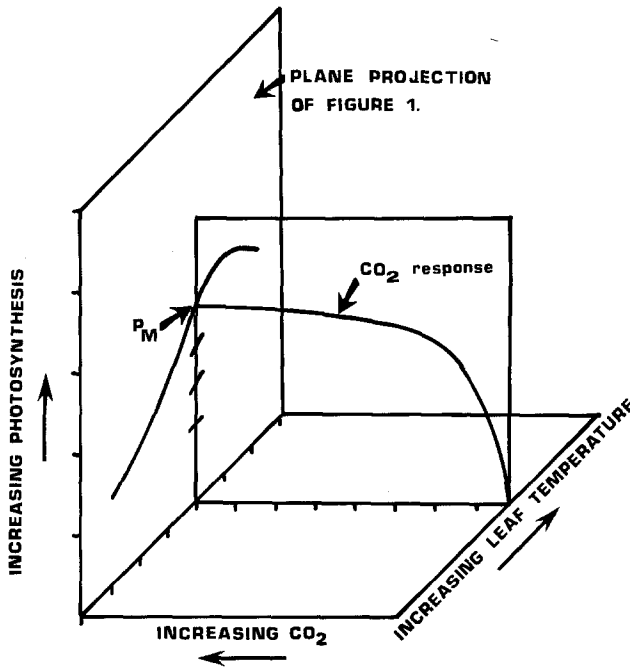
Fig. 2. Illustration of the CO_2 response described in the text as it relates to the R_M surface of Figure 1. For clarity, the several temperature curves at different light intensities have been removed from the plane projection of Figure 1

6. Summary

The equations discussed above when considered in the order 8, 9, 6, 7, 12, and 5 describe the system when oxygen concentration is maintained at 1.5%, i.e. when photorespiration does not occur. One final equation is needed to define net photosynthesis:

$$P_N = P - W \tag{13}$$

where: P_N is the rate of net photosynthesis ($nM\ cm^{-2}\ s^{-1}$).

The above formulation, while a special case for C_3 plants, should be an adequate description of photosynthesis in C_4 plants for all environmental conditions. Photorespiration must be superimposed on this description to complete a model for C_3 plants at oxygen concentrations greater than 1.5%.

Discussion

A number of simplifying assumptions allow description of the photosynthetic processes in a leaf by the set of equations given above when oxygen concentration is maintained at 1.5%. Most important among these are that respiration under these conditions is a function of only leaf temperature and can be measured by extrapolation of light or carbon dioxide response curves below zero net photosynthesis and that R_M (total resistance to gas diffusion in the liquid phase) can

be obtained from carbon dioxide response curves corrected for residual respiration (Jones and Slatyer, 1972).

It remains to elaborate the values of parameters in Equations (5), (6), (8) and (9); to establish the form of Equation (7) and determine the temperature dependencies of any parameters; to determine the light and temperature dependencies of K_C and R_M in Equation (12); and finally in the case of C_3 plants to superimpose the photorespiratory process on this scheme. Equations (5), (6), (7), (8), (9), and (13) are elaborated in a following publication based on experimental observations of photosynthesis in leaves of kidney bean seedlings (*Phaseolus vulgaris* var. Charlevois).

It is felt that a formulation such as presented here allows adequate detail to attack complicated ecological problems such as those involved in acclimation responses. When the model is applied to particular plants, it will be possible to predict photosynthesis rates as a function of the leaf environment experienced. But more importantly, information is derived that describes the structuring of underlying metabolic components at any point in time. By introducing a step change in controlled growth conditions, it will be possible to obtain a dynamic picture of acclimation in these metabolic components by applying the analysis at various times after the change. Furthermore, plasticity can be assessed for individual species by applying the analysis to individuals grown at extremes of light, of temperature, or of other environmental variables effecting acclimation. The contribution of change in any component to the photosynthesis rate or daily carbon balance (by integration) can be assessed.

References

Andrews, T., Lorimer, G., Tolbert, N.: Ribulose diphosphate oxygenase. I. Synthesis of phosphoglycolate by fraction-1 protein of leaves. Biochem. **12**, 11–18 (1973)

Arrhenius, S.: Quantitative laws in biological chemistry. London: Bell 1915

Berry, J.: The effect of oxygen on CO_2 fixation by carboxydismutase in vitro and an examination of a possible reaction of ribulose diphosphate with oxygen. Carn. Inst. Wash. Yrbk. **70**, 526–530 (1971)

Björkman, O.: Interaction between the effects of oxygen and CO_2 concentration on quantum yield and light saturated rate of photosynthesis in leaves of *Atriplex patula* ssp. *spicata*. Carn. Inst. Wash. Yrbk. **70**, 520–526 (1971)

Black, C., Fewson, C., Gibbs, M., Gordon, S.: Studies on photosynthetic processes. III. Further studies on action spectra and quantum requirements for triphosphopyridine nucleotide reduction and the formation of adenosine triphosphate by spinach chloroplasts. J. biol. Chem. **238**, 3802–3805 (1963)

Black, C., Turner, J., Gibbs, M., Krogmann, D., Gordon, S.: Studies on the photosynthetic process. II. Action spectra and quantum requirement for triphosphopyridine nucleotide reduction and the formation of adenosine triphosphate by spinach chloroplasts. J. biol. Chem. **237**, 580–583 (1962)

Bowes, G., Berry, J.: The effect of oxygen on photosynthesis and glycolate excretion in *Chlamydomonas reinhardtii*. Carn. Inst. Wash. Yrbk. **71**, 148–158 (1972)

Bowes, G., Ogren, W.: Oxygen inhibition and other properties of soybean ribulose 1,5-diphosphate carboxylase. J. biol. Chem. **247**, 2171–2176 (1972)

Bowes, G., Ogren, W., Hageman, R.: Phosphoglycolate production catalyzed by ribulose diphosphate carboxylase. Biochem. biophys. Res. Commun. **45**, 716–722 (1971)

Chartier, P.: Etude théorique de l'assimilation brute de la feuille. Ann. Physiol. vég. **8**, 167–196 (1966)

Gates, D.: Leaf temperature and energy exchange. Arch. Meteorologie, Geophysik, u. Bioklimatologie, Ser. B **12**, 321–336 (1963)

Gates, D.: Transpiration and leaf temperatures. Ann. Rev. Plant Physiol. **19**, 211–238 (1968)

Gould, J., Izawa, S.: Studies on the energy coupling sites of photophosphorylation. I. Separation of site I and site II by partial reactions of the chloroplast electron transport chain. Biochim. biophys. Acta (Amst.) **314**, 211–223 (1973)

Hall, A.: Photosynthetic capabilities of healthy and beet yellows virus infected sugar beets (*Beta vulgaris* L.). Ph.D. Thesis, University of California, Davis (1970)

Hall, A., Björkman, O.: Model of leaf photosynthesis and respiration. Perspectives in biophysical ecology, pp. 55–72. Berlin-Heidelberg-New York: Springer 1975

Horn, H.: The adaptive geometry of trees. Princeton, New Jersey: Princeton Univ. Press 1971

Johnson, F., Eyring, H., Polissar, M.: The kinetic basis of molecular biology. New York: Wiley 1954

Johnson, F., Eyring, H., Williams, R.: The nature of enzyme inhibitions in bacterial luminescence: Sulfanilamide, urethane, temperature, and pressure. J. cell. comp. Physiol. **20**, 247–268 (1942)

Jones, H., Slatyer, R.: Estimation of the transport and carboxylation components of the intracellular limitation to leaf photosynthesis. Plant Physiol. **50**, 283–288 (1972)

Kahn, J.: Evidence for a lag period in photosynthetic phosphorylation. Arch. Biochem. Biophys. **98**, 100–103 (1962)

Koffler, H., Johnson, F., Wilson, P.: Combined influence of temperature and urethane on the respiration of *Rhizobium*. J. Amer. chem. Soc. **69**, 1113–1117 (1947)

Krogmann, D.: Further studies on oxidative photosynthetic phosphorylation. J. biol. Chem. **235**, 3630–3634 (1960)

Laing, W., Ogren, W., Hageman, R.: Regulation of soybean net photosynthetic fixation by the interaction of CO_2, O_2, and ribulose 1.5-diphosphate carboxylase. Plant Physiol. **54**, 678–685 (1974)

Laisk, A.: A model of leaf photosynthesis and photorespiration. Prediction and measurement of photosynthetic productivity, pp. 295–306. Wageningen, The Netherlands: Pudoc 1970

Lommen, P., Schwintzer, C., Yocum, C., Gates, D.: A model describing photosynthesis in terms of gas diffusion and enzyme kinetics. Planta (Berl.) **98**, 195–220 (1971)

Lommen, P., Smith, S., Yocum, C., Gates, D.: Photosynthetic model. Perspectives in biophysical ecology, pp. 33–43. Berlin-Heidelberg-New York: Springer 1975

Lorimer, G., Andrews, T., Tolbert, N.: Ribulose diphosphate oxygenase. II. Further proof of reaction products and mechanisms of action. Biochem. **12**, 18–23 (1973)

Mooney, H., Harrison, A.: The influence of conditioning temperature on subsequent temperature related photosynthetic capacity in higher plants. Prediction and measurement of photosynthetic productivity, pp. 411–418. Wageningen, The Netherlands: Pudoc 1970

Nobel, P.: Introduction to biophysical plant physiology. San Francisco: Freeman 1974

Peisker, M.: A model describing the influence of oxygen on photosynthetic carboxylation. Photosynthetica **8**, 47–50 (1974)

Peisker, M., Apel, P.: Influence of oxygen on photosynthesis and photorespiration in leaves of *Triticum aestivum* L. I. Relationship between oxygen concentration, CO_2 compensation point, and intracellular resistance to CO_2 uptake. Photosynthetica **9**, 16–23 (1975)

Rabinowitch, E.: Photosynthesis and related processes, Vol. II, Part 1. New York: Interscience 1951

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

Raschke, K.: Heat transfer between the plant and the environment. Ann. Rev. Plant Physiol. **11**, 111–126 (1960)

Robinson, J., Gibbs, M.: Effects of pH upon the photosynthesis of glycolic acid and the Warburg effect in intact spinach chloroplasts. Plant Physiol. **56**, Suppl. 2, abstract 140 (1975)

Sakurai, H., Nishimura, M., Takamiya, A.: Studies on photophosphorylation. I. Two-step excitation kinetics of photophosphorylation. Plant and Cell Physiol. **6**, 309–324 (1965)

Servaites, J., Ogren, W.: Oxygen effects on photosynthesis in soybean mesophyll cells. Plant Physiol. **56**, Suppl. 2, abstract 139 (1975)

Shen, Y., Shen, G.: Studies on photophosphorylation. II. The "light intensity effect" and intermediate steps of photophosphorylation. Scientia Sinica **8**, 1097–1106 (1962)

Viil, J., Pärnik, T.: Influence of oxygen upon photosynthetic carbon metabolism at high CO_2 concentration and saturating irradiance. Photosynthetica **8**, 208–215 (1974)

Zelitch, I.: Photosynthesis, photorespiration, and plant productivity. New York: Academic Press 1971