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Integrated rate expression for the production of glucose equivalent in C_4 green plant and the effect of temperature

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Abstract. A temperature-dependent integrated kinetics for the overall process of photosynthesis in green plants is discussed. The C_4 plants are chosen and in these plants, the rate of photosynthesis does not depend on the partial pressure of O_2. Using some basic concepts like chemical equilibrium or steady state approximation, a simplified scheme is developed for both light and dark reactions. The light reaction rate per reaction center (R_1') in thylakoid membrane is related to the rate of exciton transfer between chlorophyll neighbours and an expression is formulated for the light reaction rate R_1'. A relation between R_1' and the NADPH formation rate is established. The relation takes care of the survival probability of the membrane. The CO_2 saturation probability in bundle sheath is also taken into consideration. The photochemical efficiency (ϕ) is expressed in terms of these probabilities. The rate of glucose production is given by $R_{\text{glucose}} = (8/3)(R_1' v_L)\phi(T)g(T)\,([\text{G3P}]/[P_i]^2_{\text{leaf}})_{SS} Q_{\text{G3P}\rightarrow\text{glucose}}$ where g is the activity quotient of the involved enzymes, and G3P represent glycealdehyde-3-phosphate in steady state. A Gaussian distribution for temperature-dependence and a sigmoid function for de-activation are incorporated through the quotient g. In general, the probabilities are given by sigmoid curves. The corresponding parameters can be easily determined. The theoretically determined temperature-dependence of photochemical efficiency and glucose production rate agree well with the experimental ones, thereby validating the formalism.

Keywords. Glucose equivalent production rate; C_4 green plants; exciton dynamics; dark reactions.

1. Introduction

Although experimental research on photosynthesis in green plants and related aspects gained momentum in the last few decades,[1–4] no analytical expression for glucose production rate evolved so far. This is because of the complications of glucose production process that involves light absorption by chlorophylls in thylakoid membrane, transport of energy to reaction centers, the photochemical (light) reactions, and the biosynthetic (dark) reactions (PCR or Calvin cycle). Some mathematical models involving dark-phase of photosynthesis have been put forward.[5] For the first time we have designed a single temperature-dependent rate equation including both the light reactions and the dark reactions. This offers kinetic interpretations for the production of glucose equivalent in green plants of type C_4.

2. Choice of system and related assumptions

To avoid complexity, the C_4 plants are chosen. As the rate of photosynthesis in C_4 plants is independent of the partial pressure of O_2,[3] the *competition between carbon dioxide and oxygen for the enzyme ribulose-1,5-bisphosphate carboxylase–oxygenase (Rubisco) may be neglected.*

An outline of the natural assumptions made by us is given here: (1) Systems under investigation should have high stomatal conductance and so *the ambient* CO_2 *pressure is* also *high*. Under these conditions, carboxylation is saturated and assimilation is not controlled by stomata. (2) It is taken for granted that *the plant is not under any water stress*. Thus the excessive water loss that results from a high stomatal conductance and thereby inhibits photosynthesis is considered to be compensated. Taking these two reasonable assumptions into consideration, we determine the rate of different steps of photosynthesis and the corresponding temperature dependences.

It is well known that photochemical efficiency (mole CO_2 used up per mole photon) builds up in a narrow

*For correspondence

range of temperature (5–18°C), maintains a constant value up to a certain threshold temperature that is species-dependent and generally varies between 45°C and 47°C, and ultimately decays down in a very short interval.[3]

Getting a constant efficiency over a range of temperature indicates three different aspects. (1) NADPH is consumed by different processes at proportionate rates. But temperature variation can lead to a variation of NADPH concentration. Therefore, (2) the different rate constants remains more or less same at the concerned temperature region. Besides, (3) the order with respect to NADPH would be the same for the competing processes, and the concentrations of other reactants including CO_2 remain more or less unvarying. Finally, the decay of the efficiency signifies the degeneration of the membrane.

3. Related reactions and rate equations

3.1 *The light reactions*

During the light phase of photosynthesis, light energy is absorbed by chlorophyll molecules on thylakoid membrane. This energy is transported to the reaction centers in the form of excitons. In the reaction center NADPH is produced using this energy. In our previous publications we have reported our theoretical findings on the light absorption and exciton transport in thylakoid[6a,b] membrane of green plants. We have shown that the total rate of exciton transfer ($p_{s,s'}$) from site s to another site s' can be written as a sum of contribution from coherent[7] ($p^{\text{inc}}_{s,s'}$) and incoherent[8] ($p^{\text{inc}}_{s,s'}$) transfer rate:

$$p_{s,s'} = p^{\text{coh}}_{s,s'} + p^{\text{ine}}_{s,s'}. \tag{1}$$

We have used the quantities

$$p^{\text{coh}}_{s,s'} = \frac{\tau_{\text{rel}} |V_{ss'}|^2}{\hbar^2},$$

and

$$p^{\text{inc}}_{s,s'} = 6\pi\hbar^{-3}\omega_D^{-3} N k_B T x \cdot (|\tilde{H}_{s,-s'}(s)|^2)_{t=\tau_{\text{rel}}}, \tag{2}$$

where τ_{rel} is the exciton relaxation time, of the order of 10^{-12} second (s) for a molecular crystal, $V_{ss'}$ is dipole–dipole interaction, ω_D is the Debye frequency, x is a factor of unity and $\tilde{H}_{\text{m}}(t)$ is the dressed-exciton propagator that arises from the linear exciton–phonon coupling.[8] It is evident from (2) that the incoherent transfer rate is a temperature-dependent quantity and thereby turns the total transfer rate into a temperature-dependent one. The total transfer rate from a chlorophyll molecule to its nearest neighbour was calculated. A numerical simulation was also carried out to find out the rate of reaction at reaction centers.[6b] A numerical interpolation method is adopted here to relate these two quantities. Using this relation ultimately we get the maximum value of NADPH production rate, $R_1' = 3{\cdot}235 \times 10^{-7}$ [(672·5–197·3 exp (–1·577k_t)], in mol (L of lumen)$^{-1}$ s^{-1} for unit PPFD (Photosynthetic Photon Flux Density). The net NADPH formation rate is related to the survival probability of the membrane $P_{mem}(T)$ and is given by $R_1 = R_1' P_{mem}(T)$ where

$$P_{mem}(T) = \frac{e^{-\lambda_f (T-T_f)}}{1+e^{-\lambda_f (T-T_f)}}, \tag{3}$$

in Ms^{-1}. Here λ_f is a constant and T_f is the mid-point temperature at which the thylakoid membrane undergoes degeneration. These two can be determined from photochemical efficiency curve (figure 1).

3.2 *The dark reactions*

One part of the so-called dark reactions, that is, the overall CO_2 assimilation process and glucose pro-

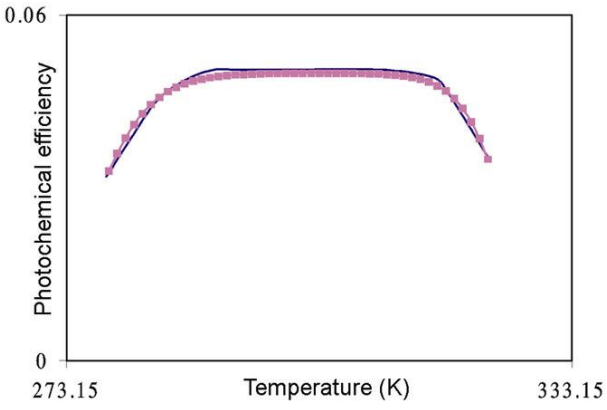

Figure 1. Temperature-dependence of photochemical efficiency (mol CO_2 per mol of photon). The solid line stands for the experimental curve (from ref. 3). The dotted line represents the calculated efficiency (reproduced with permission from *J. Phys. Chem.* 2006 **B110** 10951. Copyright 2006 American Chemical Society).

duction, occurs in mesophyll cells. The major reactions that occur in mesophyll cells are as follows:

$$CO_2(g, p_{CO_2}) \rightleftharpoons CO_2(\text{meso}) \quad (\text{overall } k_1) \tag{4}$$

$$PEP + CO_2(\text{meso}) + H_2O + H^+ \xrightarrow[\text{PEP carboxylase}]{k_2} OAA \tag{5}$$

$$OAA + NADPH \xrightarrow[\text{NADPH Malate Dehydrogenase}]{k_3} \text{Malate} + NADP^+. \tag{6}$$

Another part occurs in the bundle-sheath of chloroplast. There is a series of enzymatic reactions involved in this process. The reactions which occur in the bundle-sheath are:

$$\text{Malate} + \text{NADP+} \xrightarrow[\text{NADP-Malic enzyme}]{k_4} \text{Pyruvate} + CO_2(\text{BS}) + NADPH + H_2O + H^+ \tag{7}$$

$$RuBP + CO_2(\text{BS}) + H_2O \xrightarrow[\text{RuBP carboxylase}]{k_5} 2\ \text{3-PGA} \tag{8}$$

$$\text{3-PGA} + ATP \xrightarrow{k_6} \text{3-PGP} + ADP \tag{9}$$

$$2\ \text{3-PGP} + 2NADPH + 2H^+ \xrightarrow[\text{enzyme}]{k_7} 2\text{G3P} + 2\text{NADP+} + 2P_i \tag{10}$$

$$2\text{G3P} \xrightarrow[\text{Enzymes}]{\text{Series of reactions}} \{CH_2O\}_6 + 2P_i \tag{11}$$

$$10\text{G3P} + 6ATP \xrightarrow{\text{Series of reactions}} 6RuBP + 6ADP + 4P_i \tag{12}$$

The overall process is

$$6RuBP + 6CO_2 + 12NADPH + 12H^+ + 18ATP \xrightarrow{\text{Enzymes}} \{CH_2O\}_6 + 12NADP^+ + 12ADP + 6RuBP + 18P_i. \tag{13}$$

Obviously, 2 molecules of NADPH are required for reduction of every molecule of CO_2. The remaining 3 molecules (calculated from steady state photochemical efficiency value, 1/20) are utilized in fat biosynthesis,

$$\text{Acetyl Co-A} + 7\text{Melonyl-S-Co-A} + 14NADPH + 20H^+ \xrightarrow{\text{Enzymes}} CH_3(CH_2)_{14}COO^- + 7CO_2 + 8\text{CoA–SH} + 14NADP^+ + 6H_2O, \tag{14}$$

and nitrogenase reactions,

$$N_2 + 3NADPH + 5H^+ + 12ATP + 12H_2O \xrightarrow{\text{Enzymes}} 2NH_4^+ + 3NADP^+ + 12ADP + 12P_i. \tag{15}$$

3.3 *The simplified scheme*

A simplified reaction scheme involving only seven (groups of) reactions is constructed for the entire photosynthetic process.[9] The groupings are done by considering apparent equilibria or effective rates. The formalism needs the observed concentrations of CO_2 (BS), G3P and P_i and one experimental value ($\Delta G_E{}^S$). The choice of a few temperature parameters and exponents would complete the formalism.

To start with, there is the so-called light reaction where NADPH is produced:

$$4h\nu + NADP^+ + H^+ + 2e^- \rightarrow NADPH \quad (R_1). \tag{16}$$

The rate R_1 is determined from the numerical simulation of exciton dynamics.

A series of complicated reactions (4)–(8) keeps a constant ratio of the concentration of CO_2 in the mesophyll cells and that in the bundle-sheath. It can be shown that the total concentration of malate, OAA and PEP does not change with time. It is considered that the individual concentrations of these three intermediates as well as the concentrations of 3-PGA and RuBP to remain constant while glucose is produced at a steady rate. An explicit expression is obtained for the time-dependent concentrations of CO_2(meso) and CO_2(BS) while the reaction (8) is treated as a reversible process. The limiting concentrations (as $t \rightarrow \infty$) are calculated, and the ratio of

the limiting values is not time-dependent. Thus one can write the overall step

$$CO_2\ (\text{meso}) \rightarrow CO_2\ (\text{BS}) \quad (R_2). \tag{17}$$

The quantity R_2 is constant for a particular concentration of each of PEP, 3-PGA and RuBP. However, R_2 does not explicitly enter into our calculations.

The assimilated CO_2 in the bundle-sheath is subsequently converted to Glyceraldehyde-3-Phosphate (G3P) through reactions (8)–(10). This process is described as

$$CO_2(\text{BS}) + 2\text{NADPH} + 2H^+ + 2\text{ATP} + \text{RuBP} + H_2O \xrightarrow{k_3^{\text{eff}}} 2\text{G3P} + 2\text{NADP}^+ + 2\text{ADP} + 2P_i\ (R_3) \tag{18}$$

The effective rate constant k_3^{eff} corresponds to the condition that water is in excess and the concentrations of H^+, ATP and RuBP remain constant. However, in our calculations, the derived form of k_3^{eff} is not explicitly used, rather, R_3 is related to R_1, the overall rate of NADPH production.

The conversion of G3P to glucose $\{CH_2O\}_6$ is catalysed by a series of enzymes such as triosephosphate isomerase, aldolase, fructosediphosphatase and glucose-6-phosphatase.[10] All steps other than the fast conversion of glucose-6-phosphate to glucose by glucose-6-phosphatase are reversible in nature. Therefore, the subsequent reactions of G3P can be described in the steady state formulation with an apparent equilibrium constant Q_4 for the process

$$2\text{G3P} + E_n^{\text{act}} \rightarrow \{CH_2O\}_6 + 2P_i + E_n^{\text{act/intact}}. \quad (Q_4) \tag{19}$$

In the above, E_n is a representative enzyme involved in the conversion of G3P to $\{CH_2O\}_6$. The superscripts 'act' and 'inact' represent the activated and the inactivated forms. It is considered that the inactive form maintains equilibrium with the active form,

$$E_n^{\text{act}} \rightleftharpoons E_n^{\text{intact}} \quad (Q_5) \tag{20}$$

The quantity Q_4 shown in step (19) is given by

$$Q_4 = \frac{[\{CH_2O\}_6][P_i]^2[E_n^{\text{tot}}]}{[\text{G3P}]^2[E_n^{\text{act}}]}. \tag{21}$$

In this work, experimental ΔG value is used to determine Q_4. However, Q_5 is not used.

The reactions for fat biosynthesis and nitrogenase reactions are written in the compact form

$$2\text{NADPH} + \text{Etc.} \xrightarrow{k_6^{\text{eff}}} 2\text{NADP}^+ + \text{Etc.}' \quad (R_6) \tag{22}$$

where k_6^{eff} is an effective rate constant. In our treatment, R_6 would be related to R_3.

In the Calvin cycle the initial substrate Ribulose-1,5-biphosphate (RuBP) is taken up by Rubisco. This then reacts with CO_2 to give two molecules of G3P. Twelve molecules of G3P are produced from every 6 molecules of RuBP consumed by this process, of which two are used for the glucose production, and the remaining ten are used for regeneration of 5 molecules of RuBP. The regeneration of RuBP is represented by a simplified version of reaction (12), that is,

$$\frac{5}{3}\text{G3P} + \text{ATP} \rightarrow \text{RuBP} + \text{ADP} + \frac{2}{3}P_i \quad (R_7) \tag{23}$$

In this work, R_7 would be related to R_3.

3.4 *Rate equations*

The rate equations for the reactions (16), (18), (22) and (23) can be written as

$$R_1 = \text{d[NADPH]/d}t. \tag{24}$$

$$R_3 = \frac{1}{2}d[\text{G3P}]/\text{d}t = -\frac{1}{2}d[\text{NADPH}]/\text{d}t = k_3^{\text{eff}}[CO_2(\text{BS})][\text{NADPH}]^2 \tag{25}$$

$$R_6 = -\frac{1}{2}\,\text{d[NADPH]/d}t = k_6^{\text{eff}}[\text{NADPH}]^2. \tag{26}$$

$$\frac{\text{d[RuBP]}}{\text{d}t} = R_7 - R_3. \tag{27}$$

At the saturated concentration of CO_2 (BS), $R_6 = 3/2R_3$ so that the maximum photochemical efficiency is 0·05. This gives

$$k_6^{\text{eff}} = \frac{3}{2}k_3^{\text{eff}}[CO_2(\text{BS})]_{\text{sat}}. \tag{28}$$

As d[RuBP]/dt becomes zero in the steady state, $R_3 = R_7$. The overall rate of change of [G3P] is given by

$$\left.\frac{d[\mathrm{G3P}]}{\mathrm{d}t}\right|_{\mathrm{ex}} = 2\mathrm{R}_3 - \frac{5}{3}\mathrm{R}_7 = \frac{1}{3}k_3^{\mathrm{eff}}[\mathrm{CO_2(BS)}][\mathrm{NADPH}]^2, \tag{29}$$

where the subscript ex implies that other reactions of G3P are not considered here. Taking (26) and (28) into consideration the rate of change of [NADPH] can be written as

$$\mathrm{d[NADPH]}/\mathrm{d}t = \mathrm{R}_1 - 2\mathrm{R}_3 - 2\mathrm{R}_6 =$$

$$\mathrm{R}_1 - k_3^{\mathrm{eff}}(2[\mathrm{CO_2(BS)}] + 3(\mathrm{CO_2(BS)})_{\mathrm{sat}})[\mathrm{NADPH}]^2. \tag{30}$$

This equation relates R_1 from the light reactions with the rates of processes (18) and (22) that occur in the dark phase of photosynthesis.

3.5 *Solution of the rate equations*

3.5a *Generation of G3P:* Solution of (30) shows that the saturated concentration of NADPH is given by

$$[\mathrm{NADPH}(\infty)] = \sqrt{\frac{\mathrm{R}_1}{b}}, \tag{31}$$

where $b = 2k_3^{\mathrm{eff}}[\mathrm{CO_2(BS)}] + 3k_3^{\mathrm{eff}}[\mathrm{CO_2(BS)}]_{\mathrm{sat}}$ in $\mathrm{M^{-1}\,s^{-1}}$. Using the saturated concentration of CO_2 in bundle-sheath cell (10^{-5} M) it can be shown that $k_3^{\mathrm{eff}} = 2\mathrm{R}_2 \times 10^{12}$ in unit $\mathrm{M^{-2}\,s^{-1}}$.

The photosynthetic efficiency (ϕ) rises sharply within a narrow range of temperature and then remains stable. As it is directly related to the [CO_2(BS)], the latter must follow a similar trend with increase in temperature. A sigmoid function is chosen for the temperature dependence of [CO_2(BS)], that is,

$$[\mathrm{CO_2(BS)}] = [\mathrm{CO_2(BS)}]_{\mathrm{sat}} P_{\mathrm{sat}}(T), \tag{32}$$

where

$$P_{\mathrm{sat}}(T) = \frac{e^{\lambda_i (T - T_i)}}{1 + e^{\lambda_i (T - T_i)}}, \tag{33}$$

λ_i being a constant of the order of unity and T_i the mid-point initiation temperature in K. The initiation temperature is about 5°C.

Using (31) into (25), one obtains

$$\mathrm{R}_3 = k_3^{\mathrm{eff}}[\mathrm{CO_2(BS)}]\frac{\mathrm{R}_1}{b}. \tag{34}$$

Using the expressions for all the involved terms it can be shown that

$$R_3 = \frac{P_{\mathrm{sat}}(T)}{3 + 2P_{\mathrm{sat}}(T)} R_1. \tag{35}$$

The unit of R_3 is M $\mathrm{s^{-1}}$. The G3P production rate is $2\mathrm{R}_3$.

3.5b *Photochemical efficiency:* From the Z-scheme it is known that four photons are consumed to generate one molecule of NADPH. Reaction (18) shows that two molecules of G3P are produced from one molecule of CO_2 (BS). Therefore,

$$\phi = \frac{1}{8}\left(\frac{\text{Rate of production of G3P}}{\text{Maximum rate of production of NADPH}}\right) \times P_{\mathrm{mem}}(T). \tag{36}$$

Using (35), one easily obtains

$$\phi = \frac{1}{4}\left(\frac{P_{\mathrm{sat}}(T)}{3 + 2P_{\mathrm{sat}}(T)}\right) P_{\mathrm{mem}}(T). \tag{37}$$

In terms of ϕ, the rate R_3 is given by

$$\mathrm{R}_3 = 4\mathrm{R}_1'\phi. \tag{38}$$

3.5c *Production of glucose equivalent:* The effect of enzymes involved in process (19) is considered. It is expected that since Rubisco affects the overall activity of the Calvin cycle,[4c] the enzyme E_n involved in reaction (19) would show a similar temperature dependence. Based on the experimental findings[4a] an expression is formulated introducing a Gaussian type function which can explain the gradual rise to the maximum and a sigmoid function that accounts for the rapid drop. We write

$$g(T) \equiv \frac{[E_{\mathrm{n}}^{\mathrm{act}}]}{[E_{\mathrm{n}}^{\mathrm{tot}}]} = e^{-\kappa(T - T_{\mathrm{opt}})^2/T} \frac{e^{-\lambda_e (T - Te)}}{1 + e^{-\lambda_e (T - Te)}} \tag{39}$$

where λ_e and κ are constants, T_{opt} is the optimum temperature where the activity is maximum (about 37°C) and T_e is the mid-point temperature for the de-activation of the enzyme (about 45°C). Incorporating the factor g from (39) in (21). We get

$$[\{\mathrm{CH_2O}\}_6] = \frac{[G3P]^2}{[P_i]^2} g(T) Q_4. \tag{40}$$

As glucose is in an apparent equilibrium with G3P, so any rise in the G3P concentration will result in a proportionate change in the glucose concentration provided that the concentration of inorganic phosphate [P_i] remains constant. The rate of glucose production can be written as[9]

$$\lim_{\Delta t\to 0}\frac{\Delta[\{CH_2O\}_6]}{\Delta t}\bigg|_{\text{formation}} = \frac{Q_4 g}{[P_i]^2}\lim_{\Delta t\to 0}\frac{\Delta[\text{G3P}]^2}{\Delta t}\bigg|_{\text{ex}}. \quad (41)$$

Using the time derivatives in place of limiting values and inserting the corresponding expression of {d[G3P]/dt}$_{\text{ex}}$ we get

$$\frac{\text{d}[\{CH_2O\}_6]}{\text{d}t}\bigg|_{\text{formation}} = \frac{8}{3}R_1'\phi g\frac{[\text{G3P}]}{[P_i]^2}Q_4, \quad (42)$$

in unit Ms^{-1}.

The value of Q_4 is determined from the free energy changes ($\Delta G_E^s = \Delta G_4^0 - \Delta G_4^s = -RT\ln Q_4$) at steady state of the four relevant steps in the Calvin cycle where G3P and fructose are directly involved.[2] The reported value of ΔG_E^s is –3·5 kcal/mol. Moreover, the water activity *in vivo*[2] is also considered. This reduces ΔG_E^s to around –2·55 kcal/mol.[9b,11] This remains more or less constant over the concerned range of temperature. Thus Q_4 is obtained as a function of temperature,

$$Q_4 = \exp(-\Delta G_E^s/RT). \quad (43)$$

The expression for the rate of production of glucose equivalent in steady state (*SS*) is obtained by combining (42) and (43). The final expression is

$$R_{\text{glucose}} = (8/3)(R_1'v_L)\phi(T)g(T)([[\text{G3P}]/[P_i]^2_{\text{leaf}})_{SS}Q_4. \quad (44)$$

in unit of mol s^{-1} per m^2 of leaf area.

4. Discussion

The expression for the rate of glucose equivalent production in (44) contains the parameters (1) T_i, λ_i, T_f and λ_f in ϕ, and (2) T_{opt}, κ, T_e and λ_e in g. The selection of the parameters is discussed in the following.

4.1 *Determination of parameters for photosynthetic efficiency*

The parameter λ_I and the pivotal temperature T_i can be determined by comparing three suitable points in the beginning of the experimental plot of ϕ versus T (for $T \ll T_f$). We get λ_i = 0·29 and T_i = 277·65 that corresponds to 4·5°C.

Similarly, three points towards the end of the experimental plot (for $T \gg T_i$) give the values λ_f = 0·37 and T_f = 325·43. So, the T_f value chosen is 325·65 corresponding to 52·5°C. The temperature T_f is that temperature at which the photosynthetic rate undergoes an irreversible decay.

The theoretical plot of ϕ versus T is generated by using (37). This is shown in figure 1.

4.2 *Other temperature pivots*

The optimal temperature (T_{opt}) for the enzyme is species-dependent. The C_4 plants are adapted to higher temperatures as they grow in extreme climatic conditions. Thus these plants show an optimal growth of an enzyme activity at around 37°C. We take this temperature as the optimal temperature.

Nevertheless, the experimental glucose equivalent production rate curve is taken from ref. 4. From that curve two different values of experimental glucose production rate at two different temperature (22°C and 30°C) are taken and κ and T_{opt} are determined using those two values in (44). We find κ = 1·49 and T_{opt} = 311·47.

In a similar fashion λ_e and T_e are also determined. But in this case the chosen experimental rates are at temperatures 42°C and 46°C. We get the values λ_e = 0·48 and T_e = 318·64.

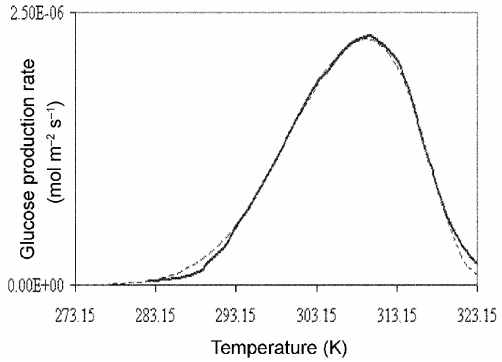

Figure 2. Glucose equivalent production rate versus temperature for an average C_4 plant. The solid line stands for the experimentally reported curve from ref. 3. The line with dots represents the theoretical curve generated from (44) (reproduced with permission from *J. Phys. Chem.* 2006 **B110** 14524. Copyright 2006 American Chemical Society).

Figure 3. Plants under investigation: (**a**) *Amaranthus cruentus* (**b**) *Flaveria trinervia* (**c**) *Panicum maximum* (**d**) *Panicum miliaceum* and (**e**) *Zea mays.*

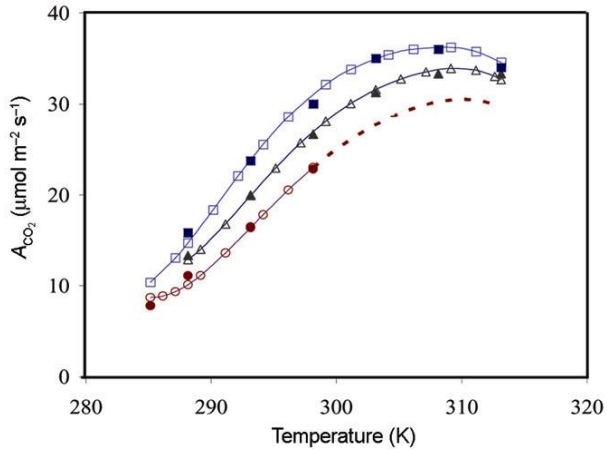

Figure 4. Calculated plots of CO_2 assimilation rate ($A_{CO_2} = 6R_{glucose}$) versus absolute temperature for maize (o), C_4 monocots (Δ) and C_4 dicots (□). Shaded symbols indicate the observed values (Reproduced with permission from 2007 *J. Phys. Chem.* **B111** 919. Copyright 2007 American Chemical Society).

The exponents κ and λ_e are finally determined from a two-dimensional least square fitting of the formation rate from (44) with the experimental curve. The optimized parameters turn out as $\kappa = 1{\cdot}4537$ and $\lambda_e = 0{\cdot}44783$ corresponding to the rms deviation $1{\cdot}01 \times 10^{-6}$.

The concentration of G3P in stroma is taken from experiment (0·032 mM)[2] and the concentration of P_i is known to be 0·1 M.[3] These values are adopted here. The plot of the glucose production rate versus temperature is shown in figure 2.

4.3 *More detailed study*

In ref. 9, we used data from ref. 3 for an average C_4 plant. Since then, the expression for the rate of glucose equivalent production has been verified for a number of different types of C_4 plants, namely; maize (*Zea mays*), C_4 monocots (*Zea mays*, *Panicum miliaceum* or broomcorn millet, *P. maximum* or Guinea grass), and C_4 dicots (*Flaveria trinervia* or clustered yellowtops and *Amaranthus cruentus* or red amaranth), for which experimental rate data are available (figure 3).[1] The agreement between the experimental and theoretical plots (figure 4) provides an evidence of the applicability of rate expression (44) to a considerable range of C_4 plants.

5. Conclusion

In this work we describe the successful solution of a set of rate laws with the target of describing the chemical kinetics of the production of glucose equivalent in C_4 plants. Reasonable simplifications are made and a simplified reaction scheme is also constructed for a very complicated process.

This work gives the rate of glucose production in C_4 plants as a function of temperature. The simple mathematical expression (44) relates the dark cycle with the light reactions, and also takes an account of complex biochemical reactions (fat biosynthesis and nitrogenase reactions). We predict that the temperature-dependence of the growth rate of all C_4 plants will be governed by the central equation, (44), or any modification thereof.

This work is based on an average intensity of solar rays as discussed in ref. 6b. The variation of the rate of photosynthesis with the intensity of the solar rays and with the partial pressure of CO_2 and O_2 in plant body are of future investigations.

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