Photosynthesis-Light Response Curve Derived from Light Absorbed in a Leaf : II. Soybean and Corn Plants

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Photosynthesis-Light Response Curve Derived from Light Absorbed in a Leaf
II. Soybean and Corn Plants

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Using the model proposed in this paper, the linear relationship of incident light with photosynthetic rates of soybean and corn leaves was obtained in low light intensity. In this range, efficiencies of light energy conversion for PhAR were 3.5-9.1 % in soybean and 7.4 -16.4 % in corn leaves. The linear relationship between light and Photosynthesis started to deviate at light intensity 0.036-0.078 cal (PhAR)/cm^2 min for soybean and at 0.073-0.116 cal (PhAR)/cm^2 min for corn. Using both these values and the chlorophyll contents of a leaf, maximum available light energies used for carboxylation by unit chlorophyll were estimated to be 210-505 cal (PhAR)/ [mg (chl) h] in soybean and 433-698 cal (PhAR)/ [mg (chl) h] in corn leaves. The maximum photosynthetic rates, saturated with light, of corn leaves were estimated to be 130 mg CO_2/(dm^2 h) (form proposed model in this study) and 189 mg CO_2/(dm^2 h) (form reciprocal equation).

INTRODUCTION

Since a leaf has a certain thickness, light absorption rates in the upper mesophyll layers of a leaf may be different from those in the lower layers.

In my previous paper (Hirota, 1987), a model which describes light absorbed in each layer of a leaf was derived from the relationship of chlorophyll content of a leaf with light transmission and reflection. That model shows that mesophyll tissues near a leaf surface struck by light absorb more light than those near the opposite side of the leaf. If photo-and enzymatic reaction rates of mesophyll tissues in a leaf are proportional to light energy absorbed, photosynthetic rate of a leaf might be proportional to light energy absorbed in the whole mesophyll layer. But Laisk's model (Laisk, 1970) of enzymatic-chemical reaction in photosynthesis indicates that a relationship between light energy absorbed and the photosynthetic rate at the reaction site shows a Blackman type response curve (Blackman, 1905). The Blackman type curve consists of two parts between light intensity and leaf photosynthetic rate, one of which is linear and another is plateu. According to Laisk's model, we can assume that chloroplasts near a lighted surface are saturated with light beyond a certain light intensity and consequently assimilate CO, at maximum, while the chloroplasts near the opposite surface are not saturated and consequently assimilate CO_2 proportionally to light energy absorbed.

In this paper, in consideration of the above facts I propose a model of the photosynthesis-light response curve of a leaf.

MATERIALS AND METHODS

Seeds of soybean (Tamanishiki) and corn (Pioneer 3424) were sown in the pot 1/5000 ***a*** fertilized as N, P and K 2 g/pot, repectively. Leaf photosynthesis was measured at the leaf stage "6 leaf" by using an assimilating chamber, the bottom covered with black beneyl film to avoid radiating the lower surface with reflected light from beneath. Air temperature in the chamber was kept $28 \pm 1°C$ by circulating the controled water.

The light absorptivities in each layer of a leaf were calculated by using the method descrived in previous paper (Hirota, 1987).

RESULTS

1. Experimental results

The relationships of light intensity with photosynthetic rates of soybean and corn leaves are shown in Fig. 1. The photosynthetic rate increased with increasing chlorophyll content of a leaf. Chlorophyll contents of leaves used were within 3.41-4.50 mg/dm^2. In the previous paper (Hirota, 1987) it was reported that the light absorptivity A of a leaf with chlorophyll content above 4 mg chl/dm^2 almost reached a plateau. Also, Table 1 showes no difference in light absorptivity among leaves of the crops used.

2. Theory and calculation

Laisk (1970) derived the relationship between photosynthetic rates and light intensity at a reaction site in a leaf. Laisk's model consists of two parts, i. e, linear and plateau, and supposes that the enzymatic reaction in the photosynthesis producing RuBP from ATP and Ru5P irreversible. This indicates that if all of the RuBP carboxylase conbine with RuBP on a certain light intensity, ATP and $NADPH_2$

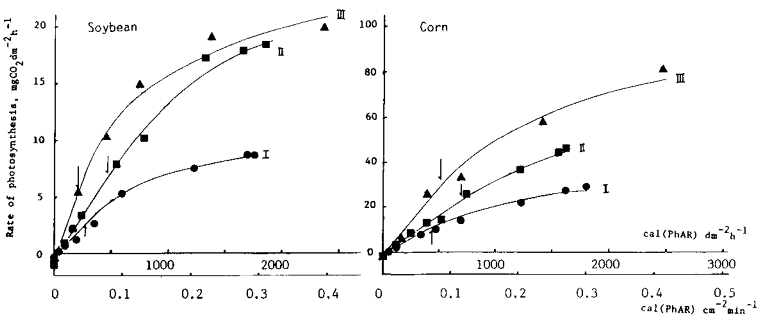

Fig. 1. Photosynthesis-light response curves of soybean and corn leaves with different chlorophyll contents. Symbols as ●, ■ and ▲ show the measured value and solid lines show the rates of photosynthesis obtained from the proposed model in this study. Roman numerals are same in Table 1.

Table 1. Relationship between chlorophyll content within a leaf and its absorptivity (A) for PhAR of soybeah and corn leaves.

	No.[1)]	chlorophyll mg/dm^2	*A*
Soybean	I	3.41	0.893
	II	3.93	0.900
	III	4.50	0.905
Corn	I	3.67	0.874
	II	3.66	0.873
	III	4.50	0.885

1) same as in Fig. 1

produced beyond this light level is useless for assimilating CO_2 because nonexistence of free RuBP carboxylase. On the other hand, a leaf photosynthetic rate increases linearly with increasing incident light to a certain light intensity as shown in Fig. 1, and then deviates from this linear line. This deviation might result from the fact that chloroplasts near a leaf surface lighted were saturated with light.

On the range of linear relation between incident light and a leaf photosynthesis, we can derive Eq. (1),

$$P_i = \phi\ A\ I_i - R \quad (1)$$

where P_i is net photosynthesis of a leaf, $mgCO_2/dm^2\,h$; I_i, light intensity, cal (PhAR)/dm^2 h; ϕ, maximum CO_2 assimilation rate per unit light absorbed by a leaf, $mgCO_2$/cal (PhAR); *A*, light absorptivity for photosynthetically active radiation (400-700 nm); *R*, respiration rate of a leaf, $mgCO_2/dm^2$ h. If we put light intensity as I_L [cal (PhAR)/dm^2 h] on which a leaf photosynthetic rate starts to deviate from the linear line, it should be supposed that mesophyll tissues in contact with the leaf surface lighted are saturated with light in the range beyond I_L. We designate this light intensity I_L as the upper limit of light intensity showing a linear relationship between light intensity and leaf photosynthesis.

We express the upper limit of light energy, which is used for carboxylation by unit mesophyll layer, by ι [cal (PhAR)/dm^2 h]. We designate ι as following. According to Laisk's theory, all of the RuBP carboxylase in the layers absorbing light energy beyond ι combine the RuBP to make RuBP carboxydismutase complex. Therefore, if these layers absorb light energy beyond ι and produce RuBP from Ru5P and ATP, RuBP is not used for reducing CO, because of nonexistence of free RuBP carboxylase. Then, ι means the maximum available light energy used for carboxylation by unit mesophyll layer. Taking into account these facts, Fig. 2 is shown to calcutate the photosynthetic rates of a leaf by using both light absorbed in each mesophyll layer and ι described above. When a leaf receives incident light I_i ($I_i > I_L$), each mesophyll layer absorbs light energy $\alpha M \times I_i$ (Hirota, 1987). Since $I_i > I_L$, the layers near the leaf surface absorb light energy more than ι. Therefore, the mesophyll layer of a leaf consists of both layers (O-M,) saturated with light and layers (M-1) unsaturated. The light energy available for carboxylation is indicated by the area surrounded by the symbols 0, ι, *C*, *B* and *A* in the Fig. 2. The net assimilation rate of a leaf at light intensity I, ($I_i > I_L$) is equal to the product of the light energy shown by this area and

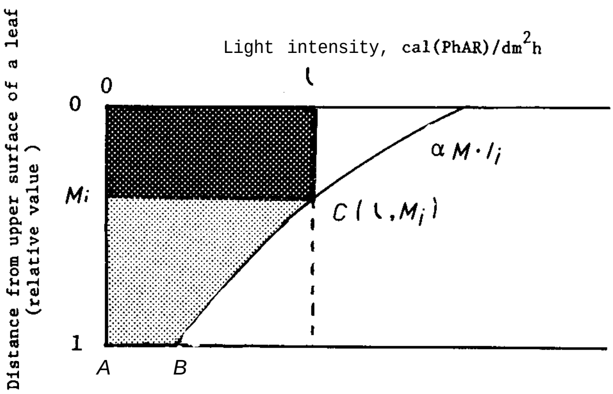

Fig. 2. Schematic illustration for estimating the rate of photosynthesis by using light energy absorbed in each layer of a leaf. Symbols as in text.

ϕ (maximum CO, assimilation rate per unit light energy absorbed by a leaf). Then we can determin ι (maximum available light energy used for carboxylation by unit mesophyll layer) as follows.

Let us select an arbitrary light intensity observed on which a leaf photosynthesis starts to deviate from the linear relationship between light intensity and a leaf photosynthesis (Fig. 1). We express this light intensity by I_{L0} [cal (PhAR)/dm^2 h] and the temporary ι by ι_0. Then we can obtain Eq. (2) showing the relationship between I_{L0} and ι_0,

$$\iota_0=\alpha M|_{M=0}\times I_{L0}, \tag{2}$$

where $\alpha M|_{M=0}$ is light absorptivity of a top mesophyll layer of a leaf obtained from Eq. (21) in previous paper (Hirota, 1987) by setting $M=0$. The ι_0 is regarded as a primary approximation of ι. According to Fig. 3, we can determine ι from ι_0. If the upper surface of a leaf receives a light I_i ($I_i > I_{L0}$), the light energy absorbed $\alpha M_{i,0} \times I_i$

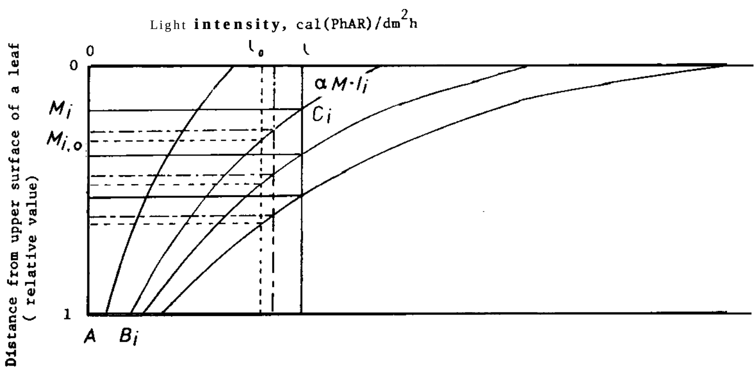

Fig. 3. Schematic illustration for estimating the value ι in Fig. 2. Symbols as in text.

by a certain layer $M_{i,0}$ in the leaf is equal to ι_0 as described above,

$$\alpha M_{i,0} \times I_i - \iota_0 = 0. \tag{3}$$

Equation (3) shows that the layers above $M_{i,0}$ in a leaf are saturated with light and those under $M_{i,0}$ are not saturated.

The primary approximation of net photosynthesis $\bar{P}_i$ (mgCO_2/dm^2 h) of a leaf at incident light intensity I_L is

$$\bar{P}_i = \phi\left\{\int_0^{M_{i,0}} \iota_0 \, dM + I_i \int_{M_{i,0}}^1 \alpha M dM\right\} - R. \tag{4}$$

The value of $\bar{P}_i$ can be made to approach P_i, a measurement of leaf photosynthesis , by using the "least square" method. If we designate the difference between $\bar{P}_i$ and P_i by d_i,

$$\Sigma d_i^2 = \Sigma(\bar{P}_i - P_i)^2 = \Sigma\bar{P}_i^2 - 2\Sigma\bar{P}_i P_i + \Sigma P_i^2, \tag{5}$$

where,

$$\bar{P}_i^2 = \phi^2\left\{\iota_0 M_{i,0}^2 + 2\iota_0 M_i I_i \int_0^{M_{i,0}} \alpha M dM + I_i^2 \left(\int_{M_{i,0}}^1 \alpha M dM\right)^2\right\},$$

$$\bar{P}_i P_i = \phi\left\{\int_0^{M_{i,0}} \iota_0 \, dM + I_i \int_{M_{i,0}}^1 \alpha M dM\right\} P_i.$$

Since Cd_i^2 in Eq. (5) is positive, we can obtain ι_0 to make Σd_i^2 minimum. That ι_0 equal to ι. Therefore, if we differenciate Σd_i^2 [Eq. (5)] with respect to ι_0 and set $d\Sigma d_i^2/d\iota_0 = 0$, we obtain Eq. (6).

$$\iota = \frac{\Sigma M_{i,0} P_i - \phi \Sigma M_{i,0} I_i \int_{M_{i,0}}^1 \alpha M dM}{\phi \Sigma M_{i,0}^2} \tag{6}$$

Then, by setting $\iota_0 = \iota$ again, we repeat to calculate ι by use of Eq. (3)~(6). We determine ι finally, when the change of ι by recalculation is in the range 1 % of ι. By using this ι, we can obtain Eq. (3)' showing a relationship between the depth M_i of the layer saturated with light in a leaf and ι.

$$\alpha M_i I_i - \iota = 0. \tag{3)'}$$

Net photosynthetic rate of a leaf is shown by Eq. (7), obtained from Eq. (4) by setting $\iota_0 = \iota$ and $M_{i,0} = M_i$.

$$\begin{aligned}\bar{P}_i = \phi\,[\,\iota M_i + I_i \exp\{-(-\ln T_{C0} + K_{TC} C)\} \\ - I_i \exp\{-(-\ln T_{C0} + K_{TC} C) M_i\} - I_i R_{C0} \exp(-K_{RC} C - K_{RM}) \\ + I_i R_{C0} \exp(-K_{RC} C - K_{RM} M_i)] - R,\end{aligned} \tag{7}$$

where T_{C0} and K_{TC} are parameters related with light transmission of a leaf. and R_{C0}, K_{RC} and K_{RM} are related with reflection (Hirota,1987); C, chlorophyll content of a leaf.

The relationship between light intensity I_L and ι at which the photosynthetic rate of a leaf starts to deviate from the linear line is shown by Eq. (2)', obtained from Eq. (2) by setting $\iota_0 = \iota$ and $I_{L0} = I_L$.

$$\iota = \alpha M|_{M=0} \times I_L. \qquad (2)'$$

The procedure described above to estimate the photosynthesis-light response

Table 2. Parameters calculated by using proposed model in this study for photosynthesis-light response curves in Fig. 1

	No.	ϕ[1]	IL[2]		ι[3]	ι_*[4]	$\phi\iota_*$[5]
		mgCO₂ / cal (PhAR)	cal (PhAR) / dm²h	cal (PhAR) / cm²min	cal (PhAR) / dm²h	cal (PhAR) / mg (chl) h	mgCO₂ / mg (chl) h
		×10⁻²					
Soybean	I	1.16	270	0.045	1032	302	3.5
	II	1.73	468	0.078	1980	505	8.7
	III	2.98	216	0.036	948	210	6.2
Corn	I	2.72	438	0.073	1626	443	12.1
	II	3.57	696	0.116	2556	698	25.0
	III	6.01	522	0.087	2184	485	29.2

Notes :
1) Maximum CO_2 assimilation rate per unit light energy absorbed by a leaf
2) Light intensitv on which linear relationshio between rates of photosynthesis and light intensity starts to deviate
3) Maximum available light energy used for carboxylation by unit mesophyll layer
4) Maximum available light energy used for carboxylation by unit chlorophyll
5) Maximum ability to assimilate CO_2 per unit chlorophyll

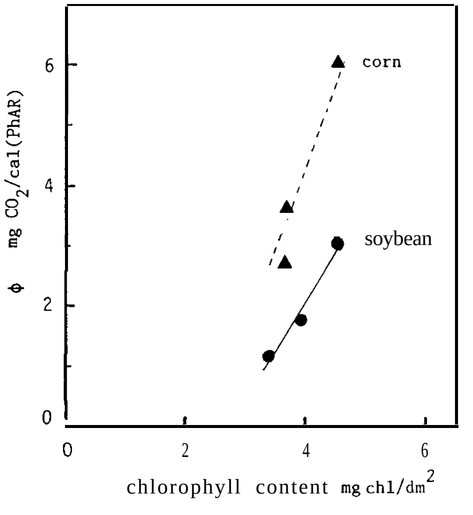

Fig. 4. Relationship of chlorophyll contents of soybean and corn leaves with maximum CO_2 assimilation rate per unit light energy absorbed by a leaf (ϕ).

curve of a leaf can be summarized as follows. First of all, we calculate ϕA and R by the use of Eq. (1) showing the linear relationship between I_i and P_i in the low light region. Next, we calculate ι from Eq. (3)~(6) by using these ϕA, R and I_L. Then we can calculate the net photosynthesis P_i of a leaf at light intensity I_i from Eq. (7). Using the above procedure, light-curve shown in Fig. 1 was obtained. The parameters ϕ and I_L used in making the light-curve are mentioned in Table 2. Figure 4 shows the relationship between chlorophyll content C of a leaf and maximum CO, assimilation rates ϕ per unit light energy absorbed by a leaf. The ϕ is proportional to the chlorophyll content on both leaves of soybean and corn.

The light intensity I_L at which the net photosynthetic rate starts to deviate from the linear relationship is 240~480 cal (PhAR)/dm^2 h for soybean leaves and *420-720* cal (PhAR)/dm^2 h for corn leaves.

In this study, we have derived ι the maximum available light energy used for carboxylation by unit layer of a leaf (Table 2). Using both ι and chlorophyll content of a leaf, we can calculate the maximum available light energy used for carboxylation per unit chlorophyll [ι_* cal (PhAR)/mg chl h] . Using the light absorption rate A of a leaf, we can rewrite Eq. (2)' as Eq. (8).

$$\iota = \frac{dA}{dM}\bigg|_{M=0} \times I_L \tag{8}$$

Deviding Eq. (8) by the chlorophyll content C (the variable M is defined as a relative value varying from 0 to 1), we can obtain Eq. (9) showing ι_*.

$$\iota_* = \frac{\alpha M}{C}\bigg|_{M=0} \times I_L . \tag{9}$$

The ι_* of the corn leaf is greater than that of soybean (Table 2).

We can obtain maximum ability to assimilate CO, per unit chlorophyll by multiplying ϕ by ι_*. As shown in Table 2, corn leaves are three times greater than soybean in $\phi\iota_*$. This is the reason why both ϕ and ι_* of the corn leaf are greater than those of soybean.

Now, a leaf photosynthetic rate saturated with light P_m and light intensity I, in that case are obtained as follows. The P_m is obtained from multiplying ϕ (maximum CO, assimilation rate per unit light energy) by ι (maximum available light energy used for carboxylation by unit layer of a leaf), because of supposing that a leaf thickness is 1.0 and its all layers are saturated with light (Table 2). The I_m is obtained from Eq. (3)' by setting $\alpha M_i = \alpha M|_{M=M}$ and $I_i = I_m$. The results obtained appear in Table 3. The saturated maximum leaf photosynthesis of soybean and corn are 34 and 131 $mgCO_2$/dm^2 h, respectively.

Table 3. Comparison between results obtained from the proposed model and obtained from the reciprocal equation”

	No.	proposed model				reciprocal equation				
		ϕ[2] mgCo2 / cal (PhAR)	P_m[3] mgCO2 / dm²h	I,“’ cal (PhAR) / cm²min	h[7]	b[5] mgCO2 / cal (PhAR)	b_*[6] mgCO2 / cal (PhAR)	P_m[3] mgCO2 / dm²h	I_m[4] cal (PhAR) / cm²min	h[7]
Soybean	I	0.012	11.94	3.92	0.996**	0.015	0.016	14.0	∞	0.993**
	II	0.017	34.12	6.05	0.997”	0.023	0.026	37.7	〃	0.995**
	Ill	0.029	27.90	4.70	0.993**	0.041	0.046	27.1	〃	0.989**
Corn	I	0.027	44.41	3.30	0.997”	0.035	0.041	55.1	∞	0.997**
	II	0.036	91.50	5.16	0.994”	0.094	0.108	189.3	〃	0.996**
	III	0.060	131.40	6.26	0.997**	0.067	0.076	166.2	〃	0.998”

Notes:
1) Equation (10) in the text
2) Same as in Table 2
3) Photosynthetic rate saturated with light, obtained from using each model. The P_m on reciprocal equation equals to b/a
4) Light intensity necessary to saturate the rate of a leaf photosynthesis.
5) Maximum CO_2 assimilation rate per unit light energy absorbed by a leaf, obtained from Ep. (10) in the text
6) Same as b in 5) but expressed as b/A, where A is the same as in Table 1
7) Index of correlation. **, significant at the 1 % level

DISCUSSION

The reciprocal equation showing the photosynthesis-light curve is

$$P_g = \frac{bI}{1+aI} \tag{10}$$

where P_g is gross photosynthesis of a leaf; I, light intensity ; a, b, constants. Parameters a and b are obtained by using the data shown in Fig. 1. The parameter b in Eq. (10) indicates the initial slope of photosynthetic rate. In order to compare b with ϕ, b in Eq. (10) was divided by the light absorptivity A as expressed in b_* (Table 3). The b_* is higher than ϕ. Marshall and Biscoe (1980) indicated that the initial slope of leaf photosynthesis obtained from the reciprocal formula was overestimated. Akita *et al.* (1968) and Chartier *et al.* (1970) demonstrated the linear relationship between light intensity and the photosynthetic rate of a leaf in low light intensities.

The product of ϕ and energy content of dry matter of a leaf gives maximum conversion rate E of light energy by a leaf.

$$E = \phi \times 0.68 \times Q \times 100,$$

where Q is the energy content of a leaf [soybean, 4500 cal/g (D. W), (Hirota *et al.* *1978)* ; corn, 4000 cal/g (D. W), (Lieth, 1968)]. The E of the soybean and corn leaves are 3.55-9.13 and 7.40-16.35 % (PhAR), respectively.

The b/a from Eq. (10) indicates the gross photosynthetic rate saturated with light. There is no difference in this study of the P_{max} estimated by either methods for soybean (Table 3). But the P_{max} of corn leaf estimated by the reciprocal equation is certainly greater than that obtained by the model in this paper. It is known that the photosynthetic rate of C_4-plant is not saturated with light in natural conditions. It is interesting to know the saturated photosynthetic rate of corn leaf comparing with the predicted values (130 $mgCO_2/dm^2$ h, from proposed model in this study ; 189 $mgCO_2/dm^2$ h, from the reciprocal equation).

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