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https://doi.org/10.5109/23843

出版情報：九州大学大学院農学研究院紀要. 31 (3), pp.191-201, 1987-03-10. Kyushu University
バージョン：
権利関係：

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J. Fac. Agr., Kyushu Univ., 31 (3),191-201 (1987)

Photosynthesis-Light Response Curve Derived from Light Absorbed in a Leaf

I. Model of Light Absorption in Each Mesophyll Layer of a Leaf

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(Received July 30, 1986)

Since a leaf has a certain thickness, each mesophyll layer in it absorbs different light energy. In this paper, by using parameters related with the light transmission and reflection of a leaf, the equation describing the absorption of light in each layer of a leaf was proposed. Spectral distribution of tobacco, soybean, corn and rice plant leaves with different chlorophyll content were measured by a spectra-photometer equipped with spherical ball and opal glass. Attenuation coefficients of visible light to chlorophyll content of a leaf on dicotyledonous plants (tobacco and soybean) were larger than that of monocotyledonous plants (corn and rice). But there was no difference of reflection coefficient in either plant type. On a leaf with high chlorophyll content, light absorption of lower mesophyll layer of a leaf was smaller than that on a leaf with low content.

INTRODUCTION

A fraction of the amount of light striking a leaf is reflected, and a fraction of it is absorbed, while the residual light passes through both sides of the leaf surface (Gates ***et al.,*** 1965 ; Sinclair ***et al.,*** 1971 ; Woolley ***et al.,*** 1971). Chloroplasts near the lighted-side of a leaf absorb more light energy than those on the opposite side, because of a certain thickness of a leaf. Photosynthetic rates of a leaf lighted from both sides on some plants (Moss, 1964 ; Tanaka and Matsushima, 1971a) are higher than those of a leaf lighted from one side only, because of the uniform light absorption in each layer within a leaf. Moss (1964) indicated that the investigation of the light-curve should take into consideration the thickness of a leaf. Yabuki and Ko (1973) indicated that the light-curve had different patterns, because the light transmission might depend on the leaf construction and incident light quality. Terashima and Saeki (1983) measured light intensity in each layer of a leaf of ***Camellia*** to estimate the effects of leaf thickness on leaf photosynthesis.

In this paper, I propose a model of light absorption in each mesophyll layer of a leaf, derived from the relationship of chlorophyll content of a leaf with its both light transmission and reflection.

MATERIALS AND METHODS

Leaves with different chlorophyll contents of tobacco (var. Samsun), corn (var. Pioneier 3424), rice (var. Toyotama) and soybean (var. Tamanishiki) plants were used for investigating the relationship of chlorophyll content with reflection and transmission of a leaf for photosynthetically active radiation (PhAR).

The spectral transmittance and reflectance of a leaf were measured by using a spectra-photometer (Hitachi EPS-3T type) equipped with integrating spherical ball and opal glass, on the wavelength 400-700 nm (Hirota ***et al.,*** 1974).

RESULTS

1. Transmittance and reflectance

Spectral distributions of transmittance $\tau_{L,\lambda}$ and reflectance r_L, of tobacco leaves are shown in Fig. 1. The patterns of spectral distribution of other crops used were similar to tobacco leaves. On the high chlorophyll content of a leaf, light absorption is large, because of its little transmittance and reflectance. And there is a little absorption in a leaf with no chlorophyll.

The transmittance T_C and reflectance R_C at visible wavelength (400-700 nm) of the incident solar radiation are calculated by Eq. (1).

$$T_C=\Sigma(I_\lambda \bullet \tau_{L,\lambda})/\Sigma I_\lambda$$
$$R_C=\Sigma(I_\lambda \cdot r_{L,\lambda})/\Sigma I_\lambda \qquad (1)$$

where I_A is spectral light intensity of solar radiation at the wavelength λ on the condition of air mass=1 (Robinson, 1966) and $\tau_{L,\lambda}$ and $r_{L,\lambda}$ are spectral transmittance and reflectance at the wavelength λ, respectively.

The relationships of chlorophyll content C of a leaf with both reflectance R_C and

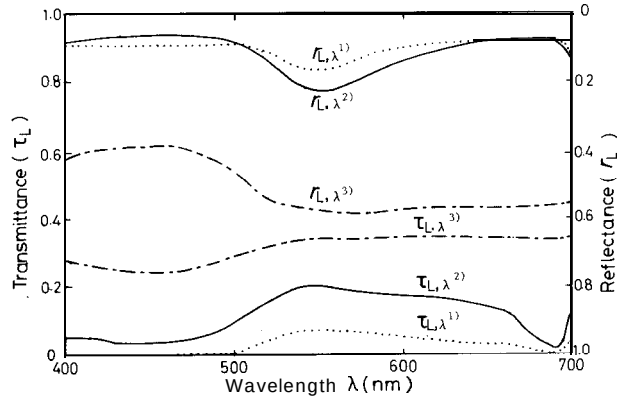

Fig. **1.** Spectral transmittance $\tau_{L,\lambda}$ and reflectance $r_{L,\lambda}$ for PhAR of a tobacco leaf. Superscripts 1, 2 and 3 denote chlorophyll contents 4, 5, 1.43 and Omg chl/dm², respectively.

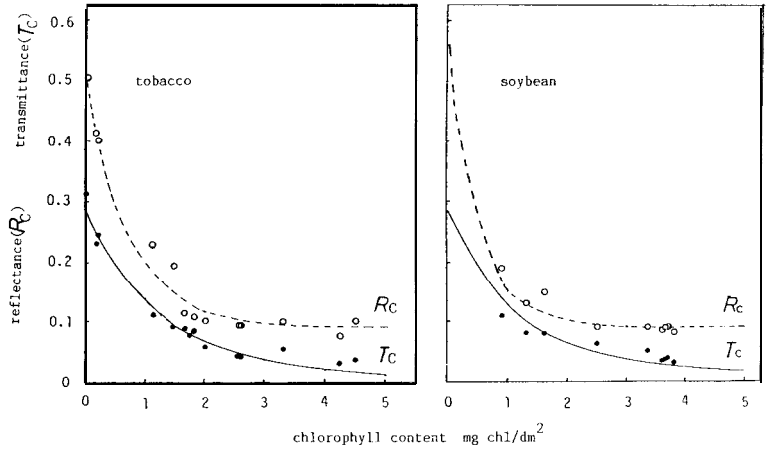

Fig. 2. Relationship of chlorophyll content within a leaf with its transmittance T_C and reflectance R_C for PhAR.

Table 1. Parameters used for characterizing the relationships of chlorophyll contents of a leaf with both transmittance T_C and reflectance R_C for PhAR of a leaf.

	transmittance		reflectance		
	T_{C0}	K_{TC}	T_{C0}	K_{RC}	r_s
Tobacco	0.281	0.684	0.418	1.395	0.09
Soybean	0.285	0.776	0.468	1.979	0.09
Corn	0.227	0.604	0.393	1.501	0.10
Rice	0.223	0.621	0.457	1.231	0.09

Notes; T_{C0} and R_{C0} are transmittance T_C and reflectance R_C of a leaf with no chlorophyll for PhAR, respectively; K_{TC} and K_{RC} are attenuation coefficients for characterizing the relationship of chlorophyll contents within a leaf with both transmittance T_C and reflectance R_C for PhAR of a leaf, respectively; r_s is the critical reflectance for PhAR of a leaf.

transmittance T_C of tobacco, soybean, corn and rice plant leaves are shown in Fig. 2. Reflectance R_C is higher than transmittance T_C regardless of the chlorophyll content. Transmittance T_C decreased with increasing chlorophyll content C. Reflectance R_C, also, decreased with increasing chlorophyll content C and converged to a 8～10 % level on not so high chlorophyll content. These converging values of reflectance can be taken as the critical reflectance of a leaf surface. The relationships of the chlorophyll content C with both transmittance T_C and reflectance R_C is approximated to the exponential function (Fig. 2). Reflectance R_C consists of both the critical reflection of a leaf surface and the reflection due to the mesophyll tissue within a leaf. The relationships of chlorophyll contents C within a leaf with both transmittance T_C and reflectance R_C are shown by Eqs. (2) and (3), respectively.

$$T_C = T_{C0} \exp(-K_{TC} C) \quad (2)$$

$$R_C = R_{C0} \exp(-K_{RC} C) + r_s \quad (3)$$

where T_{C0} and R_{C0} are transmittance and reflectance of a leaf with no chlorophyll,

respectively ; K_{TC} and K_{RC}, constants showing the relationships of chlorophyll contents with transmittance and reflectance, respectively ; C, chlorophyll content of a leaf ; r_S critical reflection of a leaf surface.

The T_{C0} and K_{TC} in Eq. 2 were determined statistically by the method of least squares using the linear relationship between chlorophyll contents C and ln of transmittance T_C in Fig. 2. The R_{C0}, K_{RC} and r_S in eq. (3) were determined by the following procedure. First of all, we regard the converged value of reflectance R_C in Fig. 2 as a critical reflectance r_S. Then, R_{C0} and K_{RC} were determined by using the linear relationship between chlorophyll contents C of a leaf and $\ln(R_C - r_S)$. The parameters obtained are shown in Table. 1.

Parameters both T_{C0} and K_{TC} which consist of transmittance T_C of dicotyledonous plant leaves (tobacco and soybean) are higher than those of monocotyledonous plant (corn and rice). But there is no difference in reflectance R_C among plant species used. Sinclair *et al.* (1971) also, reported no difference in reflectance for the visible wavelength between monocotyledonous and dicotyledonous plants.

2. **Model of light absorption in each mesophyll layer of a leaf.**

In order to make equations which describe the light flux in a leaf using the parameters in Table 1, an assumption has been made that a leaf has a certain thickness M_L and the chlorophyll is distributed in a leaf uniformly. Therefore, as shown in Fig. 3, it can be assumed that incident light on upper surface of a leaf, excepting the critical reflection r_S, attenuates in a leaf according to Beer's law. If we assume the incident light as unit, light flux at a layer A4 measured from upper surface of a leaf is shown by Eq. (4).

$$T_M = (1 - r_S) \exp(-K_{TM} M) \tag{4}$$

where K_{TM} is the extinction coefficient of light intensity in a leaf. Downward flux T_{ML} at the bottom layer of a leaf is

$$T_{ML} = (1 - r_S) \exp(-K_{TM} M_L) \tag{5}$$

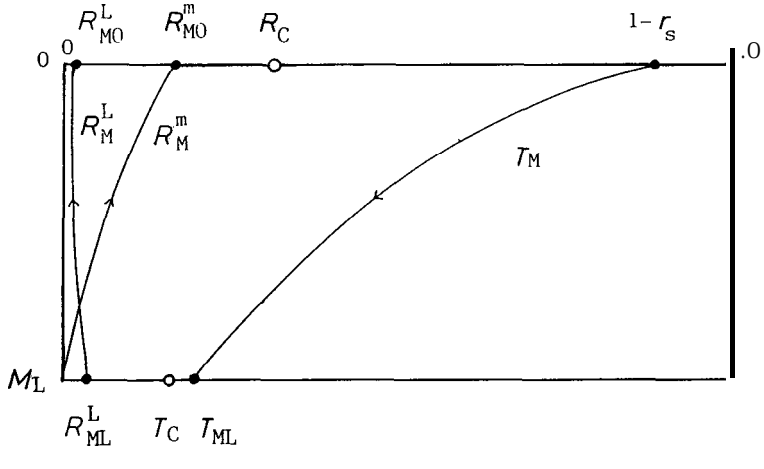

Fig. 3. Schematic illustration for evaluating PhAR absorbed by each layer of a leaf. Symbols as in text.

where M_L is the leaf thickness. The T_{ML} consists of both flux due to the critical reflection R^L_{ML} of light traveling from the leaf into the air and flux due to transmission T_C.

$$T_{ML} = R^L_{ML} + T_C. \tag{6}$$

The R^L_{ML} is shown by Eq. (7)

$$R^L_{ML} = r_{SL}\ T_{ML}. \tag{7}$$

where r_{SL} is the critical reflection of light traveling from a leaf into the air. The r_{SL} can be determined by using the general relationship (Wood, 1936) between critical reflection r_S and refractive index n_{AL} of light traveling from the air into a leaf, which is

$$r_S = \frac{(1-n_{AL})^2}{(1+n_{AL})^2}. \tag{8}$$

Substituting r_S obtained in Fig. 2 to Eq. (8), n_{AL} can be calculated. Using n_{AL}, the refractive index n_{LA} of light traveling from the leaf into the air can be calculated by Es. (9).

$$n_{LA} = \frac{1}{n_{AL}}. \tag{9}$$

Critical reflection r_{SL} of light traveling from a leaf into the air is

$$r_{SL} = \frac{(n_{LA}-1)^2}{(n_{LA}+1)^2}. \tag{10}$$

Then, substituting Eq. (9) into Eq. (10),

$$r_{SL} = \frac{(1-n_{AL})^2}{(1+n_{AL})^2}. \tag{11}$$

The r_{SL} in Eq. (11) is the same as r_S in Eq. (8).

The upward flux due to the critical reflection r_{SL} attenuates because of being absorbed by leaf tissues. This extinction coefficient can be assumed to be the same as that of the downward flux K_{TM}, because all of the light into a leaf is scattered. Then, upward flux at the layer M in a leaf is,

$$R^L_M = R^L_{ML} \exp K_{TM}\ (M\text{-}M,_). \tag{12}$$

On the other hand, in Fig. 3, the upward flux $(R_C - r_S)$ [except the critical reflection r_S at the upper surface of a leaf] consists of R^m_{M0}, due to the leaf tissue, and R^L_{M0}, due to the critical reflection of light traveling from a leaf into the air [Eq. (13)].

$$R_C - r_S = R^m_{M0} + R^L_{M0}. \tag{13}$$

Substituting R^L_{M0} obtained from Eq. (12) (in which M = 0) to Eq. (13), we can obtain upward flux R^m_{M0}, which is reflected by mesophyll tissues, at the upper surface of a leaf,

$$R^m_{M0} = (R_C - r_S) - R^L_{ML} \exp\ (-K_{TM} M_L). \tag{14}$$

Supposing a thin layer dM at layer M measured from the upper surface of a leaf, we can express upward flux, reflected by dM, by dR^m_M. Since dR^m_M is proportional to the downward flux T_M at the layer M in a leaf, we can obtain Eq. (15) by using a proportional constant a,

$$\frac{dR^m_M}{dM} = a\ T_M$$

$$= a\ (1\text{-}r,)\ \exp\ (-K_{TM} M). \tag{15}$$

Integrating Eq. (15) with respect to M from $M=0$ to $M=M_L$, we can get the upward flux R^m_{M0}, which is reflected by mesophyll tissues, at the upper surface of a leaf [Eq. (16)],

$$R^m_{M0} = \int_0^{M_m} \frac{dR^m_M}{dM}\, dM$$
$$= a\,\frac{(1-r_s)}{K_{TM}}\{1-\exp(-K_{TM}M_L)\}. \tag{16}$$

Therefore, proportional constant a in Eq. (15) is obtained from Eqs. (14) and (16),

$$a = \frac{K_{TM}[R_C - r_S - R^L_{ML}\ \exp\ (-K_{TM}M_L)]}{(1-r_S)[1-\exp\ (-K_{TM}\ M_L)]}. \tag{17}$$

Upward flux R^m_M at the layer M in a leaf is equal to the upward flux which is the integrated light being reflected by mesophyll tissues beneath the layer M. Therefore, R^m_M is obtained by integrating Eq. (15) with respect to M from $M = M$ to $M = M_L$ [Eq. (18)].

$$R^m_M = \frac{[R_C - r_S - R^L_{ML}\ \exp\ (-K_{TM}M_L)]\,[\exp\ (-K_{TM}\ M) - \exp\ (-K_{TM}\ M_L)]}{1-\exp\ (-K_{TM}\ M_L)} \tag{18}$$

The extinction coefficient K_{TM} of downward flux in a leaf is calculated from Eq. (19), which is obtained from Eqs. (2), (5) and (10).

$$K_{TM} = -\ \frac{\ln\ [T_{C0}/(1-r_S)^2] - K_{TC}\ C}{M_L} \tag{19}$$

Next, we must determine the light absorption of each layer in a leaf as following.

First of all, considering the direction of light traveling in a leaf, we determine the direction from the upper surface of a leaf to downward as positive and upward as negative. Therefore, upward flux R^L_M [Eq. (12)] and R^m_M [Eq. (IS)] are negative. If we determine the light absorption of a leaf as positive, the light absorption αM at the layer M is,

$$\alpha M = -\frac{dT_M}{dM} - (-\frac{dR^L_M}{dM}) - (-\frac{dR^m_M}{dM}) \tag{20}$$

The αM is calculated from Eq. (21) which is obtained by substituting the differentiated Eqs. (4), (12) and (18) with respect to M into Eq. (20),

$$\alpha M = K_{TM}\ \{(1-r_S)\ \exp\ (-K_{TM}M) + R^L_{ML}\ exp\ K_{TM}(M-M_L)$$
$$-\ \frac{[R_C - r_S - R^L_{ML}\ \exp\ (-K_{TM}\ M_L)]\ \exp\ (-K_{TM}\ M)}{1-\exp\ (-K_{TM}\ M_L)}\} \tag{21}$$

The light absorption A of the whole layer of a leaf is obtained by integrating Eq. (21) with respect to M from $M=0$ to $M=M_L$,

$$A = \int_0^{M_L} \alpha M\, dM$$
$$= 1 - R_C - (1-r_s)\exp(-K_{TM}M_L) + R^L_{ML}. \tag{22}$$

The light absorption A, from the surface to a layer M in a leaf is,

$$A_M = \int_0^M \alpha M \mathrm{d}M$$
$$= (1-r_s)[1-\exp(-K_{TM}M)] + R^L_{ML}[\exp K_{TM}(M-M_L) - \exp(-K_{TM}M_L)]$$
$$- \frac{[R_C - r_s - R^L_{ML}\exp(-K_{TM}M_L)][1-\exp(-K_{TM}M)]}{1-\exp(-K_{TM}M_L)} \quad (23)$$

Also, light absorption A_L from the layer M to M_L is,

$$A_L = \int_M^{M_L} \alpha M \mathrm{d}M$$
$$= (1-r_s)[\exp(-K_{TM}M) - \exp(-K_{TM}M_L)] + R^L_{ML}[1-\exp K_{TM}(M-M_L)]$$
$$+ [R_C - r_s - R^L_{ML}\exp(-K_{TM}M_L)]\frac{\exp(-K_{TM}M_L) - \exp(-K_{TM}M)}{1-\exp(-K_{TM}M_L)}. \quad (24)$$

DISCUSSION

Using parameters in Table 1 and assuming a leaf thickness $M_L = 1$, the extinction coefficients K_{TM} of light in a leaf with different chlorophyll contents were calculated from Eq. (19) (Table 2).

Profiles of light flux in a tobacco leaf obtained from Eq. (4) by using the attenuation coefficient K_{TM} in Table 2 are shown in Fig. 4. Figure 4 also shows the downward flux of light in a leaf obtained from Eq. (4), because we assumed the incident light intensity on a leaf as unit. Downward flux attenuate rapidly in a leaf with higher chlorophyll content.

Figure 5 shows both upward flux of R^m_M due to the reflection of mesophyll tissue and that of R^L_M due to the critical reflection of light traveling from the leaf to the air. The R^m_M and R^L_M were calculated from Eqs. (18) and (12), respectively. The R^m_M increased upward and R^L_M decreased upward. Both R^m_M and R^L_M of upward flux decreased upward in a leaf with higher chlorophyll content.

The light absorption rate αM in each layer of a leaf is shown in Fig. 6. Even

Table 2. Relationship between exinctino coefficie extinction r PhAR in a leaf and its chlorophyll content of several crops.

	chl mg/dm^2					
	0	1	2	3	4	5
	K_{TM}					
Tobacco	1.08	1.76	2.45	3.13	3.82	4.50
Soybean	1.07	1.84	2.62	3.39	4.17	4.95
Corn	1.27	1.88	2.48	3.08	3.69	4.29
Rice	1.27	1.89	2.51	3.13	3.75	4.37

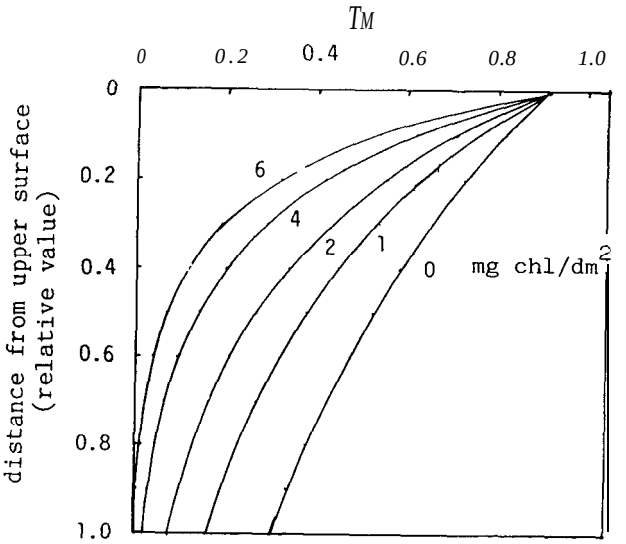

Fig. 4. Downward flux T_M of PhAR *in* a tobacco leaf.

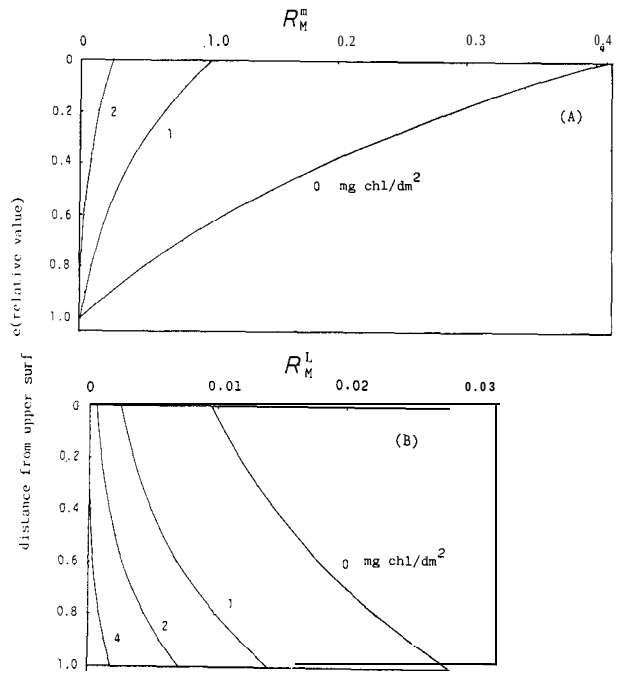

Fig. 5. Upward flux of PhAR in a tobacco leaf.
(A) shows the upward flux R_M^m due to a leaf tissue. (B) shows the upward flux R_M^L due to the critical reflection of light traveling from a leaf into the air.

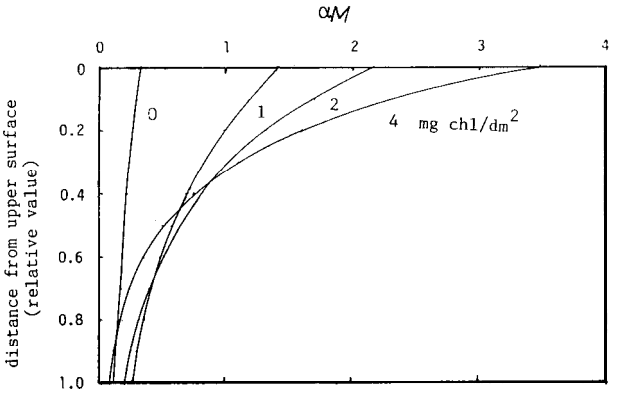

Fig. 6. Absorptivity αM for PhAR in each layer within a tobacco leaf.

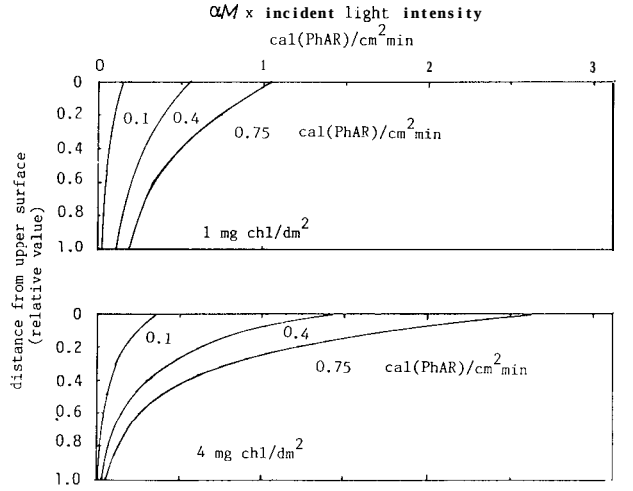

Fig. 7. PhAR absorbed by each layer of a tobacco leaf at various incident lights.

though a leaf chlorophyll content is low, each mesophyll layer absorbs light energy almost uniformly from its upper surface to the bottom. On a leaf with a higher chlorophyll content, most of the incident light is absorbed by the upper layers. On a leaf with a low chlorophyll content, however, more light is absorbed by the lower layers.

The light absorbed by each layer of tobacco leaves with chlorophyll content 1 and 4 mg/dm² are shown in Fig. 7. The upper layers of a leaf with high chlorophyll content absorb more light than lower layers. This suggests a reason for the phenomenon reported by Tanaka and Matsushima (1971b) (that abaxial surface photosynthesis of a leaf with high chlorophyll content was lower than that of a leaf with low content).

The relationships between the chlorophyll content and light absorption rate of a

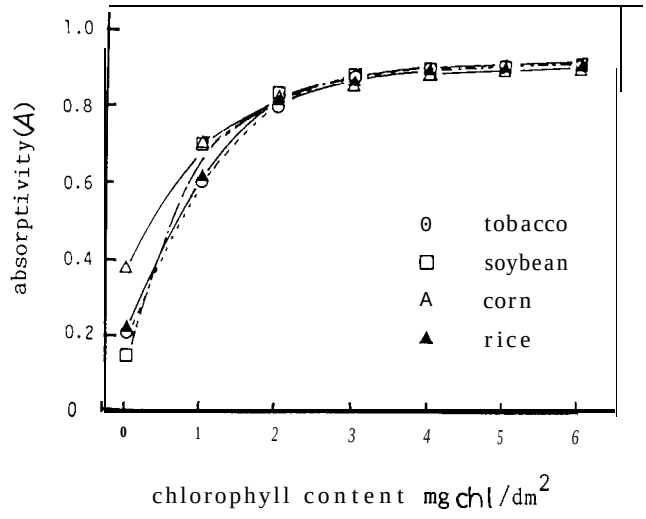

Fig. 8. Relationship between absorptivity A for PhAR of the whole layer of a leaf and its chlorophyll content.

leaf the 4 crop species used are shown in Fig. 8, which has been calculated from Eq. (22). The light absorption rate A is different among crops with a lower chlorophyll content of a leaf. It might become because of the differences in the architecture within the leaves used. This difference of light absorption rate among crops disappears beyond 4 mg chl/dm².

ACKNOWLEDGEMENT

The author wishes to thank Dr. M. Yoshida for his helpful discussion.

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