韓草誌 : 3 (2) : 77 ~85 , 1983

A Study on Photosynthetic Kinetics of Sunflower, *Helianthus annus* L.

Chang, Nam-Kee and Sung-Ha Kim
College of Education, Seoul National University, Seoul

해바라기의 光合成에 対한 動力学的 研究

張楠基 · 金成河
서울大学校 師範大学

Summary

This report gives the results of studies on the photosynthetic kinetics. Furthermore, conformity and validity of the kinetic equation are elucidated by the experiment of sunflower leaves.

The kinetic equations of photosynthesis are dirived from the equations of assimilation and dissimilation. The equations (6) and (7) are obtained by the result of this investigation. Conformity and validity of the above kinetic equations are elucidated by the fitted equation (8) on photosynthesis of sunflower leaves in relation to various environmental factors.

I. Introduction

There are many ways to study matter production, photosynthesis and their mechanisms in a plant bio-system, but certainly one of the best, that must be the final arbiter, is the study of the kinetics of mass-action itself. An enormous amount of information can be obtained from such studies, but only if we understand the subtle nuances of the theory invovled, we can properly set up and carry out the necessary experiment.

Therefore, in the present studies, the kinetic analyses have been made of mass-action and photosynthesis. In addition, the feasibility of developing a theoretical model for the prediction of net production and growth based on photosynthesis and environmental conditions was investigated. Furthermore, the kinetic equations established in this investigation were validated by the experiment of photosynthesis of sunflower leaves.

II. Methods

1. Method used in model development

Early in the development of theoretical models on the kinetics of mass-action and photosynthesis in a plant biosystem, it became apparent that a whole system diagram for a concept of the environmental factor affecting the amount of photosynthesis was needed with an intensive site.

The mathematical expression of the basic model was found in a number of reports in the literature and our own conception, and then was constructed as an original concept. Expansion of this basic concept was carried out in order to obtain other new derivative models. Any results of those methods applied to sunflower are conditional on the validity of its assumption. A major part of model validation is the determination of which variables should be introduced and should be deleted. Therefore, the kinetics of mass-action and photosynthesis was abstracted as a theoretical model expressed in the language of mathematics.

2. Experimental method of photosynthetic activities

In order to estimate the photosynthetic kinetics of a sunflower, Helianthus annus, leaf, we determined the diurnal change of photosynthetic activities under various conditions of light intensity, CO_2 concentration, H_2O content, air temperature and leaf age, and measured dark respiration rates of the leaves as related to O_2 concentration, H_2O content, air temperature and leaf age, respectively.

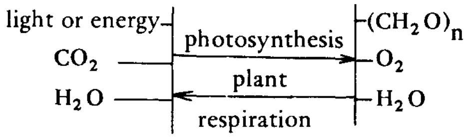
Parts of the experiment of the diurnal changes in photosynthetic activities and respiration rates were carried out in the stand from Apr. 16, to Sep. 25, 1980, together with other studies using the energy balance method and the modified half-leaf method (Nomoto & Saeki, 1969). The other parts of the experiment, concerned with temperature, CO_2 and O_2 concentration, were performed in the laboratory with the materials brought from the stand on Aug. 15 to 30.

III. Results

1. Kinetics of photosynthesis

(1) Kinetics of the trophic-function

In the process of photosynthesis and respiration in the plant, it becomes possible to establish the mechanistic equation:



(1)

where photosynthesis is the trophic-function of light, CO_2 and H_2O and respiration is the trophic-function of organic matters, O_2 and H_2O.

The kinetic equation of the photosynthetic rate can be obtained by the calculation of Chang (1977).

$$P_h = \frac{P_h C_{sI} C_{sC} C_{sH}}{(k_{pI} + C_{sI})(k_{pC} + C_{sC})(K_{pH} + C_{sH})} . \quad (2)$$

where P_h is the photosynthetic rate and P_h represents the asymptotic value of photosynthesis in the plant. In this equation, C_{sI}, Cs_C and C_{sH} represent light, CO_2 and H_2O concentrations as the trophic-variables of photosynthesis, respectively.

The kinetic equation of the respiration rate can be given by the calculation of Chang (1977).

$$-r_p = \frac{R_p C_{pM} C_{pO} C_{pH}}{(k_{rM} + C_{pM})(k_{rO} + C_{pO})(k_{rH} + C_{pH})} \quad (3)$$

where r_p represents the rate of respiration and R_p is the asymptotic value of respiration. In the equation (3), C_{pM}, C_{pO} and C_{pH} represent organic matter, O_2 and H_2O concentrations as the trophic-variables of respiration, respectively.

(2) Kinetics as the bio-function

In the equations (2) and (3), P_h and R_p are the parts of the bio-function of time and environmental factors. The kinetic equations of photosynthesis and respiration as the bio-function are modified by the calculation of Chang (1977), respectively.

$$P_h = P_{hn} \prod_{j=1}^{n} \frac{a_j \eta_j e^{-\eta_j x_j}}{(1 + a_j e^{-\eta_j x_j})^2} \cdots\cdots (4)$$

$$R_p = R_{pn} \prod_{j=1}^{n} \frac{d_j \tau_j e^{-\tau_j x_j}}{(1 + d_j e^{-\tau_j x_j})^2} \cdots\cdots (5)$$

In the equations (4) and (5), P_{hn} and R_{pn} are the asymptotic values of $\int_{-\infty}^{j} P_h(j)\,dj$ and $\int_{-\infty}^{j} R_p(j)\,dj$, respectively.

(3) Kinetics of net photosynthesis

According to the equations (2) to (5), the net photosynthesis per unit time, P_{hn}, is given by

$$P_{hn} = P_{hn} \prod_{j=1}^{n} \frac{a_j \eta_j e^{-\eta_j x_j}}{(1 + a_j e^{-\eta_j x_j})^2} \cdot \frac{C_{sI}\, C_{sC}\, C_{sH}}{(k_{pI} + C_{sI})(k_{pC} + C_{sC})(k_{pH} + C_{sH})}$$

$$R_{pn} \prod_{j=1}^{n} \frac{d_j \tau_j e^{-\tau_j x_j}}{(1\ D\ d_j w^{-\tau_j x_j})^2} \cdot \frac{C_{pM}\, C_{pO}\, C_{pH}}{(k_{rM} + C_{pM})(k_{rO} + C_{pO})(k_{rH} + C_{pH})} \cdots\cdots (6)$$

When the bio-variables of P_{hn} have the definite values, the equation (6) is given by

$$P_{hn} = \frac{P_{hn}\, C_{sI}\, C_{sC}\, C_{sH}}{(k_{pI} + C_{sI})(k_{pC} + C_{sC})(k_{pH} + C_{sH})} - \frac{R_{pn}\, C_{pM}\, C_{sC}\, C_{sH}}{(k_{rM} + C_{pM})(k_{rO} + C_{pO})(k_{rH} + C_{pH})} \cdots (7)$$

2. Conformity and validity of the kinetics

(1) The photosynthetic rate as the trophic-function the sunflower leaves which excised from 10th nodes counted from the top of the plant were used as materials. In the limited stand, the mean photosynthetic activity at 300ppm CO_2 and 27.0±1.5°C during the experimental period is nearly a trophic-function of light intensity. The photosynthesis-light curve of sunflower leaves is shown in Fig. 1. The photosynthetic rate was saturated with a light intensity of about 1.0 cal cm^{-2} $min.^{-1}$.

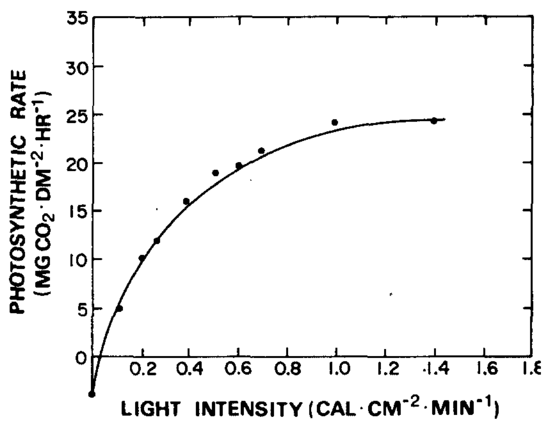


Fig. 1. Photosynthetic rate of sunflower leaves as a trophic-function of light intensity.

According to the results of Fig. 1, the kinetic equation which is fitted to the formula (2) is

$$P_h = \frac{35.2\ C_{sI}}{0.28 + C_{sI}}$$

The effect of CO_2 concentration on the rate of photosynthesis was investigated in the laboratory. In Fig. 2, the net CO_2 exchange rates measured under 1.0 cal cm^{-2} $min.^{-1}$ and at $27.0 \pm 1.5^{\circ}C$ are plotted as a function of an average CO_2 concentration of the air at the inlet and the outlet of the assimilation chamber. The photosynthetic rate was saturated at about 800ppm of CO_2 concentration and over. The CO_2 compensation point was found at 11ppm. Theoretical relationship between photosynthetic activities and CO_2 concentration can be obtained by the equation (2). This equation is

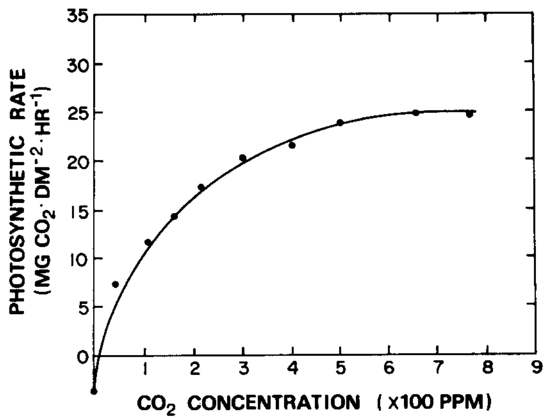


Fig. 2. Photosynthetic rate of sunflower leaves as a trophic-function of CO_2 concentration.

$$P_h = \frac{35.2\ C_{sC}}{0.013 + C_{sC}}$$

In order to obtain photosynthesis-water content curve, we adjusted the different water content of the field soil. The mean photosynthetic activities were determined at intervals of two hours in the field. Parts per maximum water-holding capacity of the field soil were estimated in the laboratory with the soil samples brought from the stand. Fig. 3 shows the photosynthesis-water content curve at 300ppm of CO_2 concentration. The equation fitted to Fig. 3 is

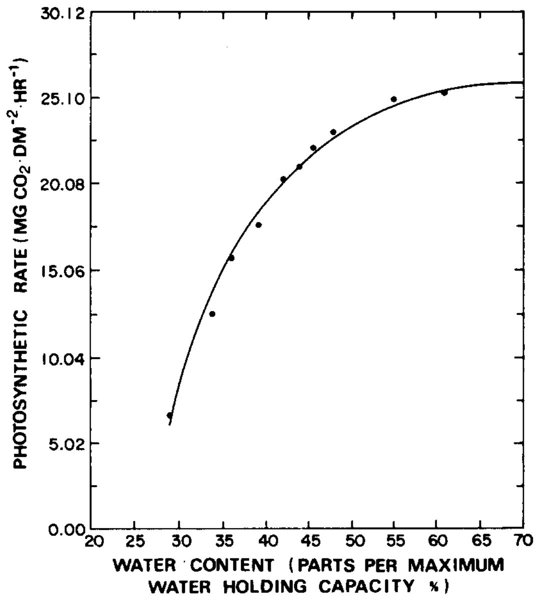


Fig. 3. Photosynthetic rate of sunflower leaves as a trophic-function of water content in the soil.

$$P_h = \frac{35.2\ (C_{sH} - 25.0)}{10.9 + (C_{sH} - 25.0)}$$

In the case of this experiment, the kinetic equation of photosynthesis of sunflower leaves as the trophic-function is

$$P_h = \frac{35.2\ C_{sI}\ C_{sC}\ (C_{sH} - 25.0)}{(0.28 + C_{sI})\ (0.013 + C_{sC})\ [10.9 + (C_{sH} - 25.0)]}$$

(2) Some bio-variables of photosynthesis

In the case of this experiment, the kinetics of photosynthesis of sunflower leaves is studied by the diurnal change of photosynthetic activities as the bio-function of air temperature and leaf age. In order to obtain photosynthesis-temperature curve, we adjusted the temperature of air passing through the assimilation chamber to 15°C – 45°C with 2.5°C or 5.0°C differences. The net CO_2 exchange rates were measured under 1.0 cal cm^{-2} min^{-1} and at 300ppm CO_2. The result of this experiment is given in Fig. 4. The optimal temperature for photosynthesis of sunflower leaves used in this experiment was found to be approximately 28.5°C.

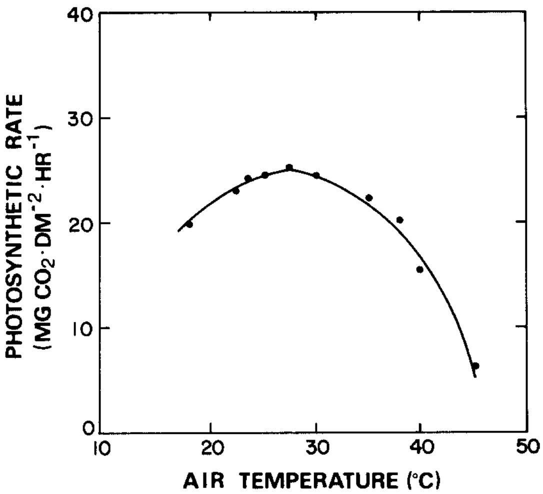


Fig. 4. Photosynthetic rate of sunflower leaves as a bio-function of air temperature.

As shown in Fig. 5, photosynthesis-leaf age curve of sunflower leaves at light saturation, 300ppm CO_2 and 27.0±1.5°C was obtained as the result of a bio-function of time. The optimal leaf age for photosynthesis of sunflower leaves was found to be about 10 days after unfolding. Conformity and validity of the equation(4) are demonstrated by the curves of Figs. 4 and 5.

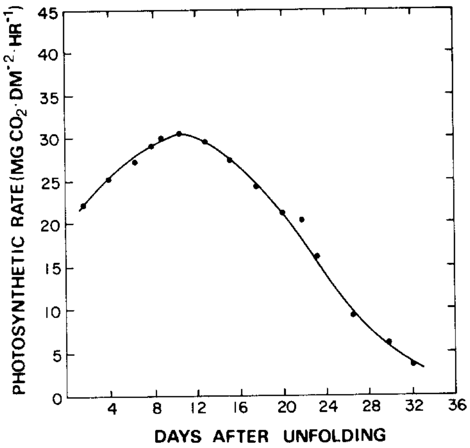


Fig. 5. Photosynthetic rate of sunflower leaves as a bio-function of leaf age.

(3) The rate of respiration as the trophic-function

Since the change of the amount of substrate for respiration can not be adjusted by the artificial methods, the experiment for respiration-substrate curve is very difficult. However, the respiration rate must be a trophic-function of substrate concentration for respiration of sunflower leaves.

In this study, respiration-oxygen and water curves of sunflower leaves at 27.0±1.5°C were obtained and shown in Figs. 6 and 7, respectively. According to the equation (3), these relationships are represented as

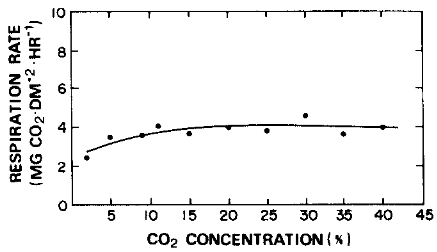


Fig. 6. Respiration rate of sunflower leaves as a trophic-function of O_2 concentration.

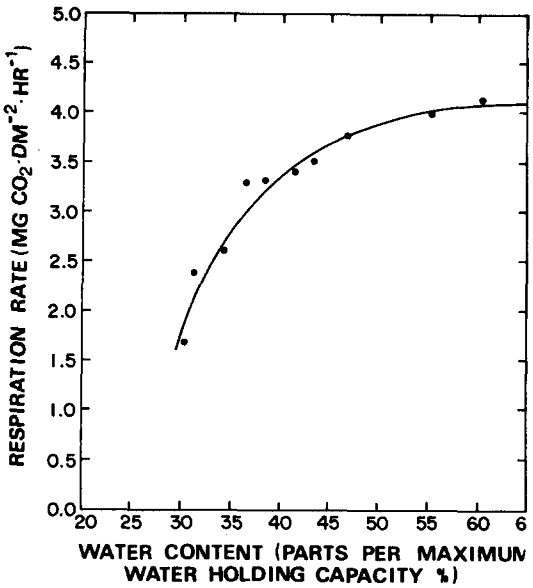


Fig. 7. Respiration rate of sunflower leaves as a trophic-function of water content in the soil.

$$-r_p = -\frac{4.2\,C_{pO}}{1.3 + C_{pO}}$$

$$-r_p = -\frac{4.2\,(C_{pH} - 25.0)}{3.9 + (C_{pH} - 25.0)}$$

The kinetic equation of the respiration rate of sunlower leaves as a trophic-function of O_2 and H_2O concentration is

$$-r_p = \frac{4.2\,C_{pO}\,(C_{pH} - 25.0)}{(1.3 + C_{pO})\,[3.9 + (C_{pH} - 25.0)]}$$

(4) Respiration rate as a bio-function

In this investigation, the kinetics of respiration of sunflower leaves is elucidated by the change of the dark respiration rate as a bio-function of air temperature and leaf age. Air temperature was changed from 15°C to 45°C during the respiration measurement. The respiration-temperature curve took a similar characteristic pattern in comparison with the photosynthesis-temperature curve. The result is given in Fig. 8. The asymphtotic value of the respiration

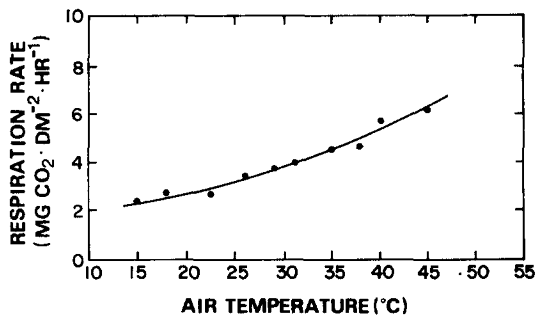


Fig. 8. Respiration rate of sunflower leaves as a bio-function of air temperature.

rate as a bio-function of air temperature could not be found in the range from 15°C to 45°C, but should be shown at 45°C and over. The respiration-leaf age curve of sunflower leaves at 27.0±15.°C is represented in Fig. 9. The maximum value of respiration was found at about 10 days after unfolding. Conformity and validity of the equation(5) are demonstrated by the curves of respiration-temperature and -leaf age of Fig. 8 and Fig. 9, respiectively.

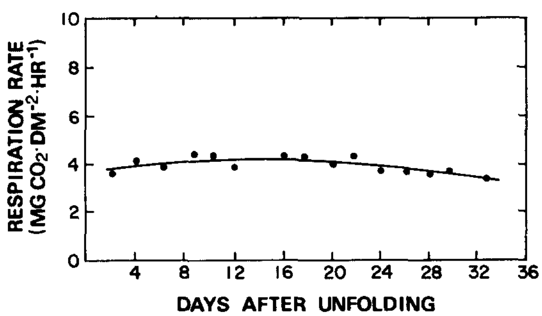


Fig. 9. Respiration rate of sunflower leaves as a bio-function of leaft age.

(5) Net photosynthesis of sunflower leaves

The equation of net photosynthesis of sunflower leaves used in this experiment is derived from the equation (7). The equation obtained is as follows:

$$P_{hn} = \frac{35.2\, C_{sI}\, C_{sC}\, (C_{sH} - 25.0)}{(0.28 + C_{sI})\,(0.013 + C_{sC})\,[10.9 + (C_{sH} - 25.0)]} - \frac{4.2\, C_{pO}\,(C_{pH} - 25.0)}{(1.3 + C_{pO})\,[3.9 + (C_{pH} - 25.0)} \quad \cdots\cdots (8)$$

IV. Discussion

An organism can be considered as one macromolecular system which has a very multiple structure. From this point of view, the metabolic action of one organism is interpreted by the same mass action as one molecular enzyme has. This theoretical concept is applied to establish the kinetic equations of assimilation and dissimilation. The assimilation and dissimilation are divided in two parts of a bio-function and a trophic-function, respectively, and have the characteristics of their kinetics. The kinetic equation of photosynthesis which is assimilation of light, CO_2 and H_2O is derived from the equation of assimilation;

$$H_2O + CO_2 + \text{light energy} \xrightarrow{\text{leaf}} (CH_2O)_n + O_2 + H_2O$$

The photosynthetic equation which presented the relationship between photosynthetic rate and light entersity was obtained by Tamiya (1951) and conformed to Monsi & Saeki (1953). This equation coincides with the equation (2) obtained by us; Under the environmental condition of a certain state except for light irradiation,

$$P_h = \frac{P_h\, C_{Si}}{k_{pI} + C_{sI}} = \frac{\frac{P_h}{k} C_{sI}}{1 + \frac{1}{k_{pI}} C_{sI}}$$

where P_h and k_{pI} are represented by a certain value such as a constant. Therefore, the above equation is changed into

$$P_h = \frac{bI}{1 + aI}$$

Kinetic models have been presented by Rabinowitch (1951) to account the rate of photosynthesis as a function of incident radiation, and these various models led to quadratic equations are equivalent to a part of the equation (2), respectively. The effect of light intensity on net photosynthesis by various species at 30°C and 300ppm CO_2 in the air (Hesketh, 1963; Hesketh & Moss, 1963) has shown the same curves in comparison with the equation (2), and with the photosynthesis-light curve of sunflower leaves. According to Gaastra (1959), the tendency of changes of net photosynthesis for intact young spinach plants in relation to CO_2 concentration at different light intensity might be expected from the equation (2) and correspond to the photosynthesis-CO_2 curves of sunflower leaves.

Moss (1963), Hofstra & Hesketh (1969), Murata & Iyama (1963), Decker (1959), Hesketh (1967) and Joliffe & Tregunna (1968) reported the effect of temperature on net photosynthesis in single leaves of maize, bermuda grass, tobacco and wheat at 300ppm of CO_2 in the air at high illuminance, respectively. These results agree with a quadratic tendency to data of sunflower of the equation(4). In the case of the bio-function, it has been known that mass-action of most plants varies with time, pH and temperature (Bonner & Galston, 1952; Devlin, 1969; Odum, 1971; Chang & Yoshida, 1973). The curves of these activities against time, pH and temperature usually exhibit a maximum, whose location varies widely from plant to plant.

The kinetic equations on mass-action and photosynthesis are validated by the resulted of the experiment on the effect of photosynthesis and respiration of sunflower leaves due to various environmental factors, and applied to their investigation.

V. 摘 要

本 報告는 光合成의 動力学에 관하여 研究한 結果이며 더욱 動力学式의 타당성과 確実性을 해바라기의 光合成実験으로 究明되었다.

光合成의 動力学式은 物質의 同化作用과 異化作用의 数式化로 부터 유도되었으며 그 結果는(6), (7)式과 같다. 한편 해바라기를 材料로 한 諸環境條件에 관계하는 光合成実験 結果로 얻어진 (8)式에 의하여 動力学式에 대한 타당성이 입증되었다.

VI. Literature cited

1. Chang, N.K. 1977. The sigmoid kinetics of mass-action and photosynthesis based on influx and efflux in a plant bio-system. Kor. J. Ecol. 1: 3-10.
2. Chang, N.K. & S. Yoshida 1973. Studies on the gross metabolism in a Sasa paniculata type grassland. I. The theoretical analysis applied to the estimation of the gross assimilation. J. Japan. Grassl. Sci. 19: 107-134.
3. Decker, J.P. 1959. Some effects of temperature and carbon dioxide concentration on photosynthesis of Mimulus. Plant Physiol. 34: 103-106.
4. Gaastra, P. 1959. Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal resistance. Meded. Landbouwhogesch. Wageningen. 59: 1-68.
5. Hesketh, J.D. 1963. Limitations to photosynthesis responsible for differences among species. Crop Sci. 3: 493-496.
6. Hesketh, J. D. 1967. Enhancement of photosynthetic CO_2 assimilation in the absence of oxygen, as dependent upon species and temperature. Planta 76: 371-374;
7. Hesketh, J.D. & D.N. Moss 1963. Variation in the response of photosynthesis to light. Crop Sci. 3: 107-110.
8. Hofstra, G. & J.D. Hesketh 1969. Effect of emperature on the gas exchange of leaves in the light and dark. Planta 85: 228-237.
9. Joliffe, P.A. & E.B. Tregunna 1969. Effect of temperature, CO_2 concentration, and light intensity on oxygen inhibition of photosynthesis in wheat leaves. Plant Physiol. 43: 902-906.
10. Monsi, M. & T. Saeke 1953. Uber den Lichtfactor in den Planzengesellshaften und seine Bedeutung fur die Stoffproduktion. Jap. J. Bot. 14: 22-52.
11. Moss, D.N. 1963. The effect of environment on gas exchange of leaves. Conn. Agr. Exp. Sta. New Haven, Bull. 664: 86-161.
12. Murata, Y. & J. Iyama 1963. Studies on the photosynthesis of forage crops. II. Influence of air-temperature upon the photosynthesis of some forage and grain crops. Crop Sci. Soc. Jap. 31: 315-322.
13. Nomoto, N. & T. Saeke 1969. Dry matter accumulation in sunflower and maize leaves as measured by an improved half-leaf method. Bot. Mag. Tokyo. 82: 20-27.

14. Rabinowitch, E.I. 1951. Photosynthesis and related processes. Vol. 2, Part 1. Wiley (Interscience), New York.

15. Tamiya, H. 1951. Some theoretical notes on the kinetics of algal growth. Bot. Mag. Tokyo. 64: 167-173.