

PHOTOSYNTHESIS OF A SOYBEAN SINGLE LEAF IN RELATION TO LIGHT INTENSITY AND LEAF TEMPERATURE

Yonny Koesmaryono¹, Daijiro Ito², Hideki Sugimoto², Tetsuya Haseba², and Haruo Suzuki³

¹Bogor Agricultural University, Bogor 16143, Indonesia

²College of Agriculture, Ehime University, Matsuyama 790, Japan

³Faculty of Agriculture, Kagawa University, Takamatsu 761-07, Japan

ABSTRACT

The photosynthesis of a single leaf of soybean fitted to non-rectangular hyperbola. The initial slopes values of the models, which expressed the quantum yield of photosynthesis under low irradiances varied with leaf temperature (ranged of 0.051 - 0.110 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$), but there were no certain tendency. The values of maximal photosynthesis were strongly affected by leaf temperature (ranged of 17.0 - 51.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and irradiances (ranged of 20.1-51.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) as well. Meanwhile, the variation in convexity of light curve may associated with the physical diffusion resistance of measured leaf. In this study, the convexity index ranged between 0.30 and 0.93 and between 0.73 and 0.92 for different leaf temperatures and different growth irradiances, respectively. Soybean exhibited the leaf temperature photosynthetic response as quadratic and the optimum temperature for photosynthesis laid about 30°C.

Key words : soybean single leaf, light response curve, leaf temperature response curve, non-rectangular hyperbola.

BASTRAK

Photosintesis sehelai daun kedelai dalam hubungan dengan intensitas cahaya dan suhu daun

Pola fotosintesis sehelai daun kedelai dalam hubungan dengan intensitas cahaya mengikuti model hiperbola non-rektangular. Nilai kemiringan awal dari model, yang menggambarkan besarnya fotosintesis per energi yang dipakai pada keadaan intensitas cahaya rendah, bervariasi menurut suhu daun (berkisar antara 0.051 - 0.110 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$), tetapi tidak menunjukkan kecenderungan tertentu. Nilai maksimum fotosintesis sangat dipengaruhi oleh suhu daun (berkisar antara 17.0 - 51.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) dan intensitas cahaya (berkisar antara 20.1 - 51.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Sementara itu, variasi kelengkungan kurva cahaya diduga berkaitan erat dengan resistensi difusi fisik dari daun. Pada studi ini, index kelengkungan berkisar antara 0.30 hingga 0.93 untuk perbedaan suhu daun dan antara 0.73 hingga 0.92 untuk perbedaan intensitas cahaya bagi pertumbuhan. Model pengaruh suhu daun terhadap respon fotosintesis pada daun kedelai adalah kudratik dengan suhu optimum bagi fotosintesis pada suhu 30°C.

Kata kunci : sehelai daun kedelai, kurva respon cahaya, kurva respon suhu daun, hiperbola non rektangular.

INTRODUCTION

Photosynthesis by green plants consumes light, carbon dioxide and water to produce oxygen, carbohydrates, and chemical energy. Photosynthesis is the most important process in plant by which provides the major input of free energy into the biosphere. Some of the free energy stored in photosynthetic assimilates is then transferred in the respiration process to high energy compounds that can be used for growth and maintenance processes of plant (Jones, 1992).

The rate of net photosynthesis (P_n) is then defined as the difference between the gross rate carbon dioxide fixation (P_g) and the rate of respiratory carbon dioxide (R). Those two processes are important factors to all aspect of plant growth, yield and adaptation. Many of the individual photosynthesis reactions take place in specialized organelles called chloroplast, within the leaf mesophyll cells (Gaastra, 1963; Jones, 1992).

According to Gaastra (1963) and Jones (1992), photosynthesis can be treated as simplified three separate components, viz: (a) *light reactions* or photochemical process, in which radiant energy is absorbed and used to generate the high energy compounds ATP (adenosine triphosphate) and NADPH (reduced nicotinamide adenine dinucleotide

phosphate); (b) *dark reactions*, which include the biochemical reductions of CO_2 to sugars using high energy compounds generated in the light reactions; and (c) *transporting process or supply of CO_2* from the ambient air toward the site of reduction in the chloroplast.

Light curves of photosynthesis which represent relation between photosynthetic rates and the quantity of light available to the plants was investigated for the first time in 1866 by Wolkoff (Rabinowitch, 1951; Höxtermann, 1992). Since that time photosynthetic light responses have been reviewed by many researchers. On this matter, Rabinowitch (1951) has developed several kinetic models to show the relationship between photosynthetic rate and light intensity. It was noted that all the kinetic models used in this term lead to be a rectangular hyperbolic light curves. All derivations of light curve equations, however, were based on the assumption of uniform light absorption, and are therefore strictly applicable only to optically thin layers of photosynthesis sites.

Though Rabinowitch (1951) insisted that deviation from his models may appears with maximum deviation 10% at 75% absorption, Peat (1970) has proven that fitting to the asymptotic curve (non-rectangular hyperbola) gave a consistently better than the rectangular hyperbola for photosynthetic rate data of a single leaf of tomato in relation to light intensity. In addition, Marshall and Biscoe (1980), Terashima and Saeki (1985) and Johnson *et al.* (1989) also suggested that the most useful general form of light curve equation is the non-rectangular hyperbola.

On the other hand, relating to the photosynthetic light response whatever the photosynthetic light curves take places, Ito and Haseba (1994) who worked on egg plant and cucumber leaves suggested that within the low light intensity, until the range of $500 \mu\text{m quanta m}^{-2} \text{s}^{-1}$, the photosynthetic light curves fit to be linear.

It is well known that photosynthesis is very responsive to temperature. Because of photosynthesis is an approximately linear sequences of reactions, the response of net CO_2 uptake to temperature is the summation of multiple effects of temperature upon individual steps of the photosynthetic process and this response interacts strongly with other environmental factors, especially light intensity and CO_2 concentration (Berry and Raison, 1981).

According to Berry and Raison (1981), the leaf temperature photosynthetic curves generally, tends to be a quadratic with one peak at certain point as optimum leaf temperature. At strongly rate-limiting light intensity the response of photosynthesis to temperature is dominated by an effect of temperature on the efficiency of light utilization.

These studies were conducted to measure the effects of different leaf temperature on the light curve of photosynthesis of soybean single leaf and to determine the photosynthetic leaf temperature response curves.

MATERIALS AND METHODS

Culture

The pots culture were conducted at experimental farm of College of Agriculture, Ehime University, Matsuyama, Japan. The pot size were about 8 liter (21 cm diameter and 23 cm height) and Wagner pots of 1/2000a. The determinate soybean [*Glycine max.* L. (merr.)] cultivar Fukuyutaka was used in these experiments. Sowing date were on June 30 and July 14, 1995. Prior to planting adequate fertilizer of N , P_2O_5 , K_2O and lime were applied on soil of each pot. The seeding rate was three per pot, which it were thined two weeks after sowing into one plant per pot. Then, after four weeks from sowing date (prior to flowering stage), plant were placed under 100%, 50% and 25% of irradiance at out door condition. Water was supplied as needed to keep adequate soil moisture.

Measurement methods

Measurement of photosynthetic light and temperature curves of a single leaf were conducted in laboratory. Assimilation chamber was made from acrylic sheet (3 mm thickness) with size $35 \times 30 \times 10$ cm. This chamber was set in a water bath chamber which have space at left, right and upper side to circulate adequate water from refrigerated cooling bath (ENDOCAL-NESLAB,PTE-8). The circulated water has function to control the leaf

temperature that was measured at assimilation chamber. Inside the assimilation chamber, it installed in front of inlet air two mini fan to get constant air flow on leaf surface as 0.5 m sec^{-1} . One air pump was used to flow the air from outside which provide CO_2 for assimilation. The flow of air controlled by slider transformer electric current by which air pump have work. After passed the cleaner box, the air was flowed to assimilation chamber. One or two flow-meter were used to measure the flow rate of air before enter to the assimilation chamber.

In this experiment, the assimilation chamber was irradiated with five incandescent lamps (500 W in power of each). The layer of water (about 10 cm thickness) was installed beneath those lamp as filter to frotict from other artificial light. The radiation intensity over the leaf specimen in the chamber was controlled by changing the voltage of electric currents of lamps using slider transformer. The dermination of radiation intensity inside the assimilation chamber have been done before the experiment run using radiometer (LI-COR, LI-190SB).

Leaf temperature was measured at a center of abaxial side of the leaf specimen, while air temperature was measured beneath the leaf at the position between and chamber base. Inlet air temperature was also measured. Thermocouples (fine cooper-constant $0.1 \text{ mm } \varnothing$) have been used to measure leaf and air temperature. The temperature sensors were connected to data logger (YOKOGAWA, $\mu\text{R } 180$). Gas exchanges measurement between inlet and outlet was measured using Infra-red Gas Analyzer (HORIBA, ASSA-1610). Further photosynthetic rate was determined by the following equation (Ito and Haseba, 1994):

$$P_n = \frac{C_i - C_0}{10^6} \times \frac{44}{22.4} \times F \times 60 \times 10^3 \times \frac{100}{A} \times \frac{300}{C_0} \times \frac{273}{273 + t}, \text{ or become}$$

$$P_n = \frac{9.65 \times 10^5 F (C_i - C_0)}{A \times C_0 \times (273 + t)}$$

Whereas : P_n : Net photosynthetic rate ($\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$)
 ($1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1} = 0.6313 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
 C_i, C_0 : Inlet and outlet CO_2 concentration (ppm)
 F : Flow rate of air (1 min^{-1})
 A : Area of leaf specimen (cm^2) and t : Inlet air temperature ($^\circ\text{C}$)

Further, the photosynthetic observation data were fitted into non-rectangular model and rectangular model for comparison. The non-rectangular models were calculated used the model developed by Marshall and Biscoe (1980) as follow :

$$\Theta P_g^2 - (\phi I + P_{\max}) + \phi I P_{\max} = 0, \text{ or become}$$

$$P_g = \frac{(\phi I + P_{\max}) - \sqrt{(\phi I + P_{\max})^2 - 4\Theta \phi I P_{\max}}}{2\Theta}$$

whereas : P_g : Gross photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and $P_g = P_n + R_d$
 I : Irradiances ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$);
 ϕ : Initial slope of photosynthesis which represent the quantum yield ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)
 Θ : Dimensionless parameter, which determines the convexity of curve
 P_{\max} : The asymptotic value of P_g at saturating irradiance ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

While the rectangular of Michaelis-Menten models were calculated used the model as follow (Tamiya, 1951):

$$P_g = \frac{bI}{(1 + aI)}$$

Whereas : P_g : Gross photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and $P_g = P_n + R_d$;
 I : Irradiances ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) ;
 a and b : Constants which characterize the shape of the curve

RESULTS

Light curves of photosynthesis

The result of experiments concerning the light curves of photosynthesis of a single leaf shown in Fig. 1 until Fig. 11. Fig. 1 and 3 show the photosynthetic light curves which were fitted into rectangular hyperbola. However, Fig. 2 and Fig. 4 until Fig. 10 show the light curve of photosynthesis were fitted into non rectangular hyperbola. Base on the non-rectangular hyperbola, the important parameter of models of different leaf specimen listed in Table 1. Regarding to the photosynthesis model, the results showed that light curve of photosynthesis of soybean were better fit into non-rectangular model than rectangular one. In addition, the results in Fig. 2, Fig. 4 until Fig. 10 and Table 1 show that leaf temperatures affect the light response curve of gross photosynthesis which were indicated by variation in initial slope, convexity and P_{max} . Nevertheless, from those three parameters seem to be that P_{max} was most influenced by different leaf temperature, while the two others seem to be more independent.

Leaf photosynthesis in response to growth irradiances

As well as being influenced by current environment, the rate of leaf photosynthesis is also effected by different irradiance in which the leaf was grown. This phenomenon can be seen in soybean leaf as shown in Fig. 11 and Fig.12 for gross photosynthesis and net photosynthesis, respectively. The results showed that the saturating light intensity and maximum photosynthesis rate in soybean were a function of the irradiance received during growth. The higher the growth irradiance is the higher the photosynthetic rate of a single leaf.

Leaf temperature curves of photosynthesis

Leaf temperature response curves for net photosynthesis ($P_{n, \text{max}}$) at light intensity of $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ were obtained for leaves grown under different irradiances. The pattern of curves were quadratic with peak at around 30°C (Fig. 13) The quadratic equation for predicting $P_{n, \text{max}}$ from leaf temperature (TL) were determined as follow :

for 100% irradiances : $P_{n, \text{max}} = -0.1045 \text{ TL}^2 + 6.0015 \text{ TL} - 56.245$ ($R^2 = 0.904$)

for 50% irradiances : $P_{n, \text{max}} = -0.0447 \text{ TL}^2 + 2.5229 \text{ TL} - 18.415$ ($R^2 = 0.963$)

for 25% irradiances : $P_{n, \text{max}} = -0.0349 \text{ TL}^2 + 2.1181 \text{ TL} - 18.766$ ($R^2 = 0.936$)

DISCUSSION

Concerning to the relation between photosynthesis processes and its environment, one of the widely used concept is Blackman's postulate. Although Blackman's concept of limiting factor is not as strictly valid as postulated originally, information about the nurture of limiting processes can, nevertheless, be obtained by studying the effects independently varied CO_2 concentration, light intensity, and temperature upon the over-all rate of photosynthesis (Rabinowitch, 1951 ; Gaastra, 1963).

In this regard, the response curve of photosynthesis to light has usually been assumed to be a rectangular hyperbola, following the theoretical derivations of Rabinowitch (1951). A rectangular hyperbola is defined by three parameters, there are initial slope of the curve,

which proportional to the maximum quantum yield of photosynthesis; the half-saturating light intensity; and $P_{n, \max}$ the limiting rate in strong light. Nowadays, the new approaches obtained that the asymptotic curve of non rectangular hyperbola was better fitted to the light curve response of photosynthesis (Marshall and Biscoe, 1980; Terashima and Saeki, 1985 ; Jhonson *et al.*, 1989 ; Hashimoto and Aoki, 1995). In all derivations of rectangular models have been found that photosynthetic rates under low and high irradiances showed over-estimate results and the convexity also lower than a non rectangular models. This phenomena also found in soybean as shown in Fig.1 and Fig.3. Thus, irrespective to the leaf temperature, all light response curves were better fitted to the non-rectangular hyperbola (Fig. 2 and Fig. 4 until Fig. 11).

Table 1. Parameter for non-rectangular model of photosynthetic light response curves of a soybean single leaf.

Date of observation	Soybean of specimen	Leaf temperature (°C)	Dark respiration ($\mu\text{mol m}^{-2}\text{S}^{-1}$)	Initial slope, ϕ ($\mu\text{mol m}^{-2}\text{S}^{-1} / \mu\text{mol m}^{-2}\text{S}^{-1}$)	Convexity Φ	P_{\max} ($\mu\text{mol m}^{-2}\text{S}^{-1}$)
1995, Aug. 14-16	① 3rd node of 7 nodes	30	0.49	0.051	0.83	29.3
		35	0.91	0.057	0.86	36.9
		40	0.73	0.048	0.91	30.5
1995, Aug. 25	② 7th node of 12 nodes	30	1.15	0.082	0.56	51.4
		35	2.75	0.076	0.72	46.1
		40	4.87	0.110	0.30	38.5
1995, Aug 30-31	③ 10th node of 12 nodes	30	1.06	0.066	0.72	38.5
		35	1.83	0.066	0.72	34.7
		40	3.00	0.067	0.51	24.9
1995, Sep. 6-7	④ 7th node of 15 nodes	25	0.86	0.066	0.69	27.8
		30	1.23	0.051	0.30	297
		35	2.04	0.074	0.74	29.7
		40	3.08	0.052	0.93	17.0
1995, Sep. 21-23	⑤ 8th node of 16 nodes	25	0.97	0.062	0.92	23.1
		30	0.44	0.056	0.88	31.2
		35	1.41	0.060	0.81	30.2
		40	2.28	0.060	0.68	24.6
1995, Sep. 17-18	⑥ 14th nodes of 14 nodes	25	1.28	0.081	0.83	47.2
		30	1.67	0.080	0.77	51.4
		35	2.57	0.066	0.86	42.4
		40	3.55	0.070	0.85	42.2
1995, Oct. 6-8	⑦ 12th node of 14 nodes	25	0.41	0.073	0.73	21.5
		30	1.00	0.063	0.92	25.5
		35	1.41	0.051	0.90	20.6
		40	2.08	0.055	0.79	21.7
1995, Sep. 14-16	⑧ 13th node of 15 nodes	25	0.21	0.062	0.86	20.1
		30	0.81	0.072	0.89	24.6
		35	1.42	0.064	0.88	24.1
		40	2.38	0.060	0.89	21.6

Note : ① was vegetatif; ② and ③ were flowering and pod formation, ④, ⑤, ⑥, ⑦ and ⑧ were pod filling; ⑦ was grown under 50% irradiance and ⑧ was grown under 25% irradiance

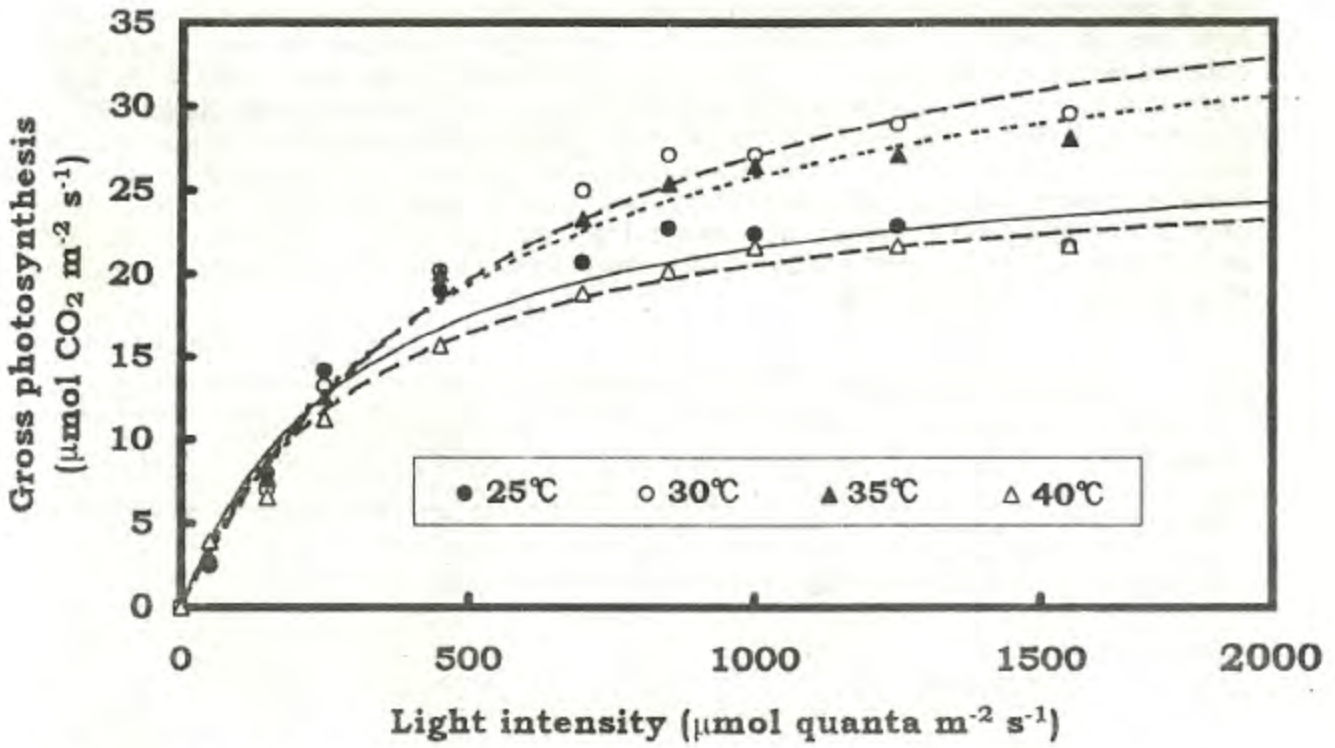


Fig 1. Gross photosynthetic light response curves at different leaf temperature fitted into rectangular model (leaf specimen no.5)

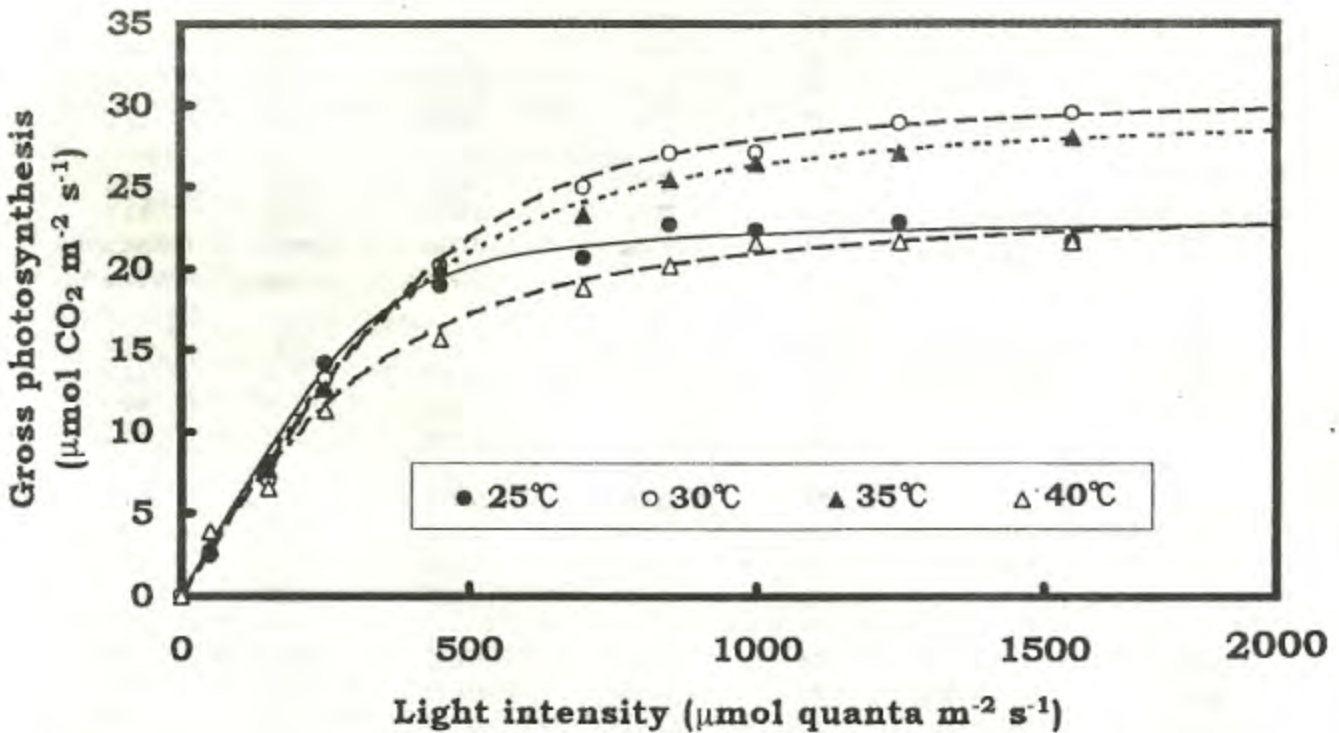


Fig.2. Gross photosynthetic light response curves at different leaf temperature fitted into non rectangular model (leaf specimen no.5)

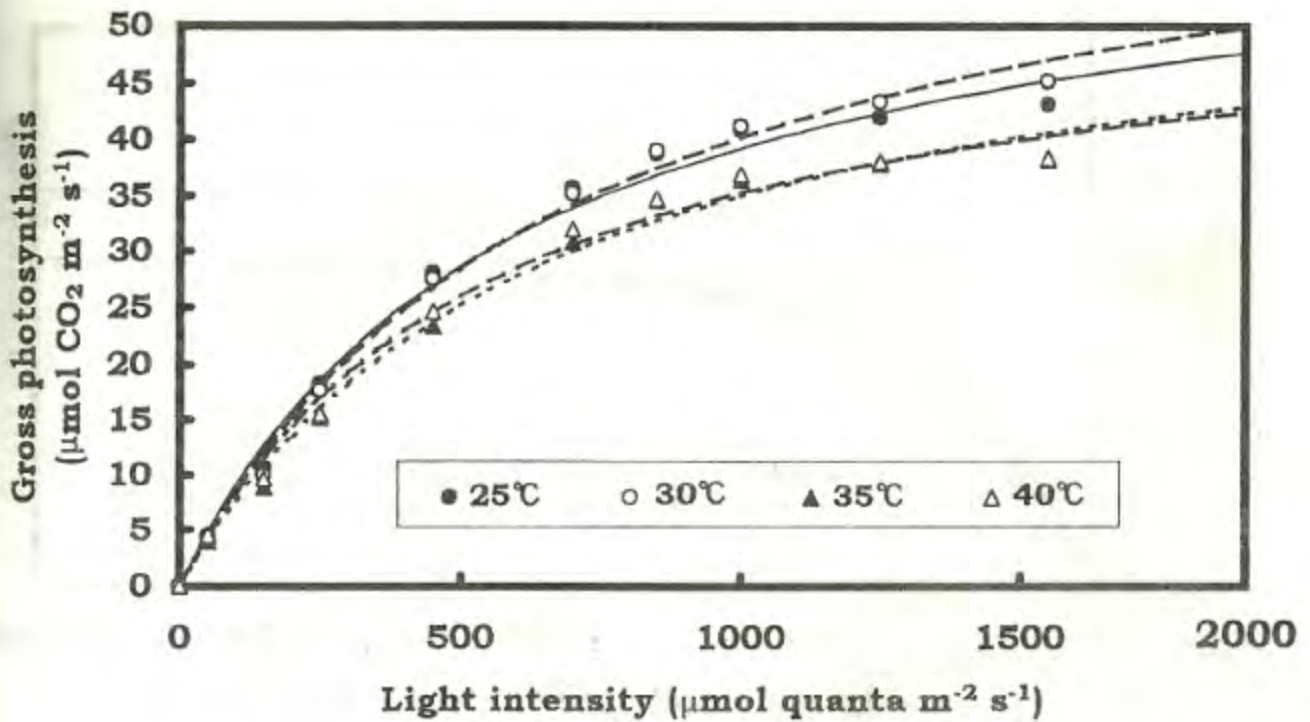


Fig.3. Gross photosynthetic light response curves at different leaf temperature fitted into rectangular model (leaf specimen no.6)

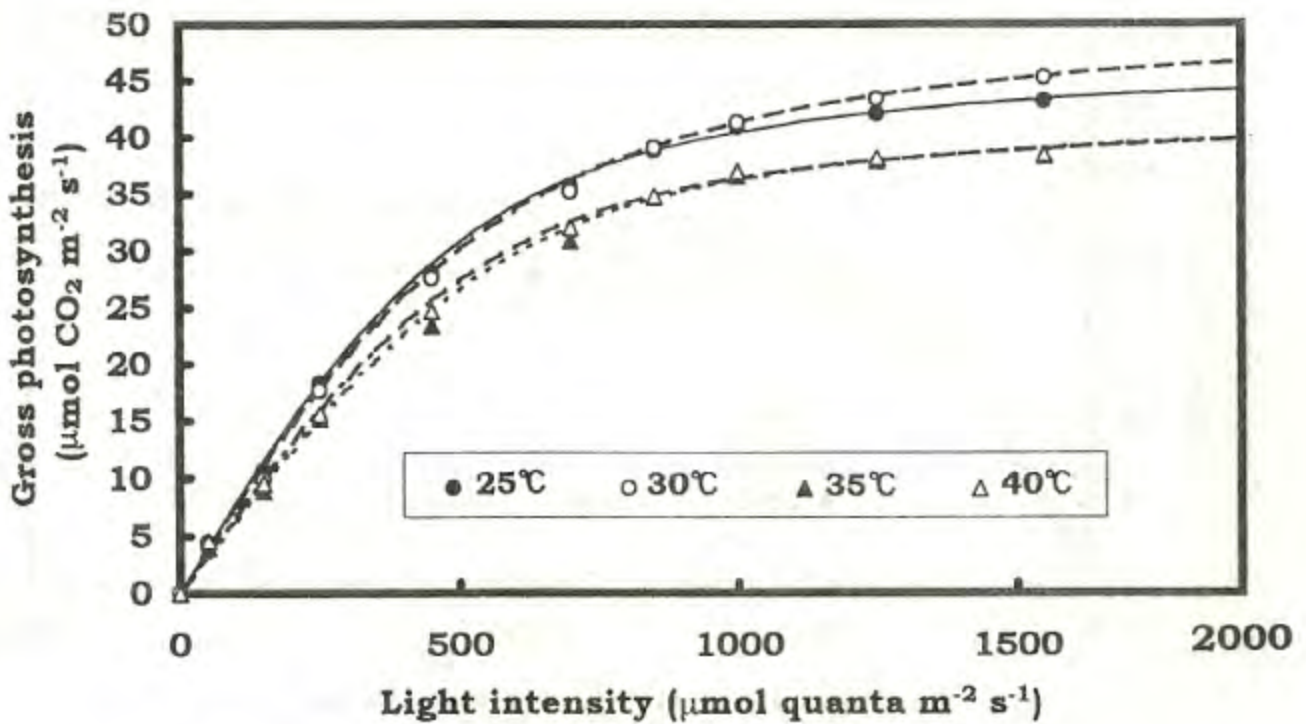


Fig.4. Gross photosynthetic light response curves at different leaf temperature fitted into non rectangular model (leaf specimen no.6)

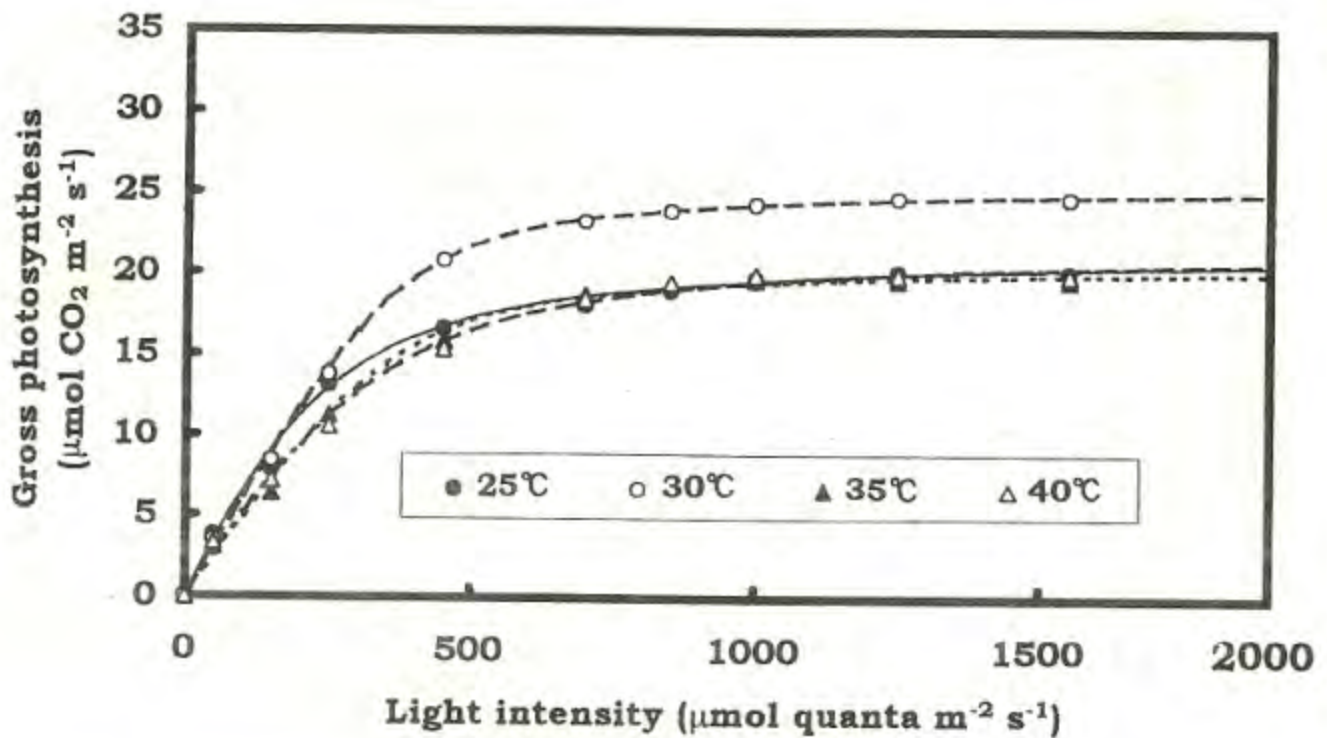


Fig 5. Gross photosynthetic light response curves at different leaf temperature fitted into non-rectangular model (leaf specimen no.7)

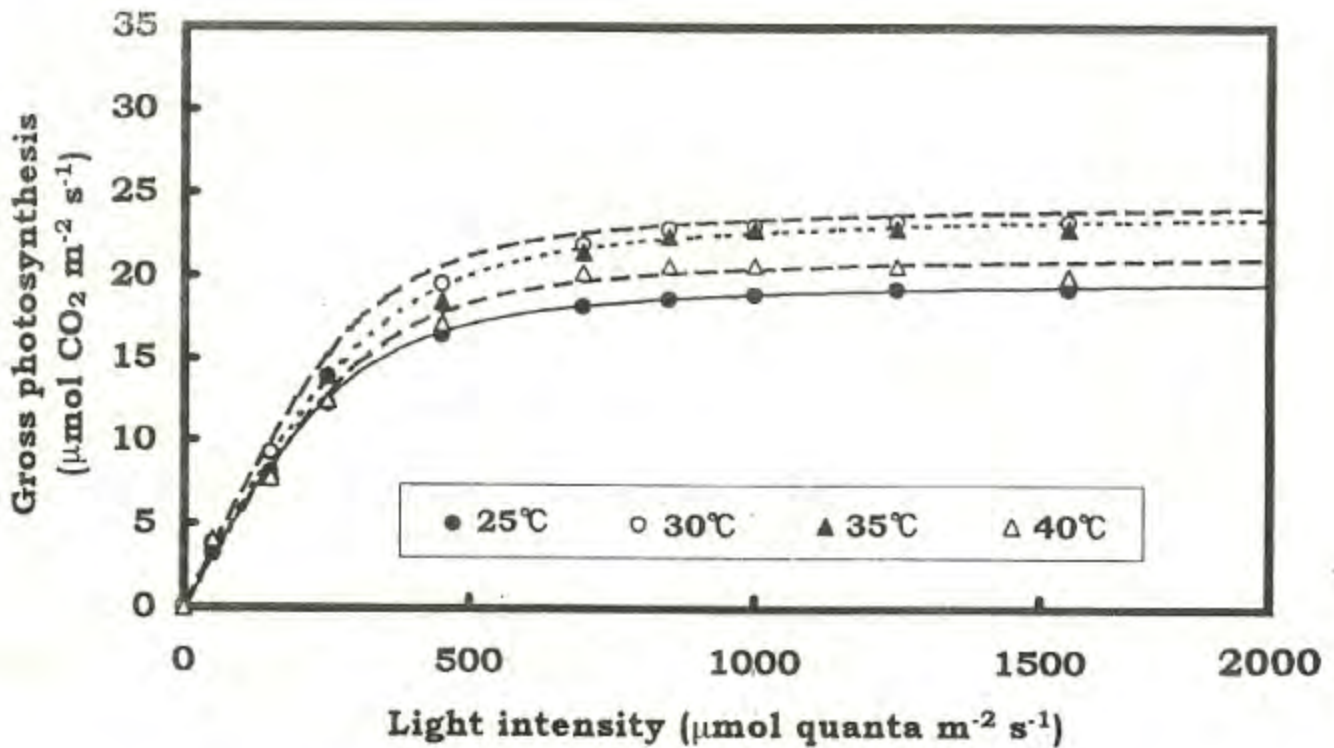


Fig.6. Gross photosynthetic light response curves at different leaf temperature fitted into non rectangular model (leaf specimen no.8)

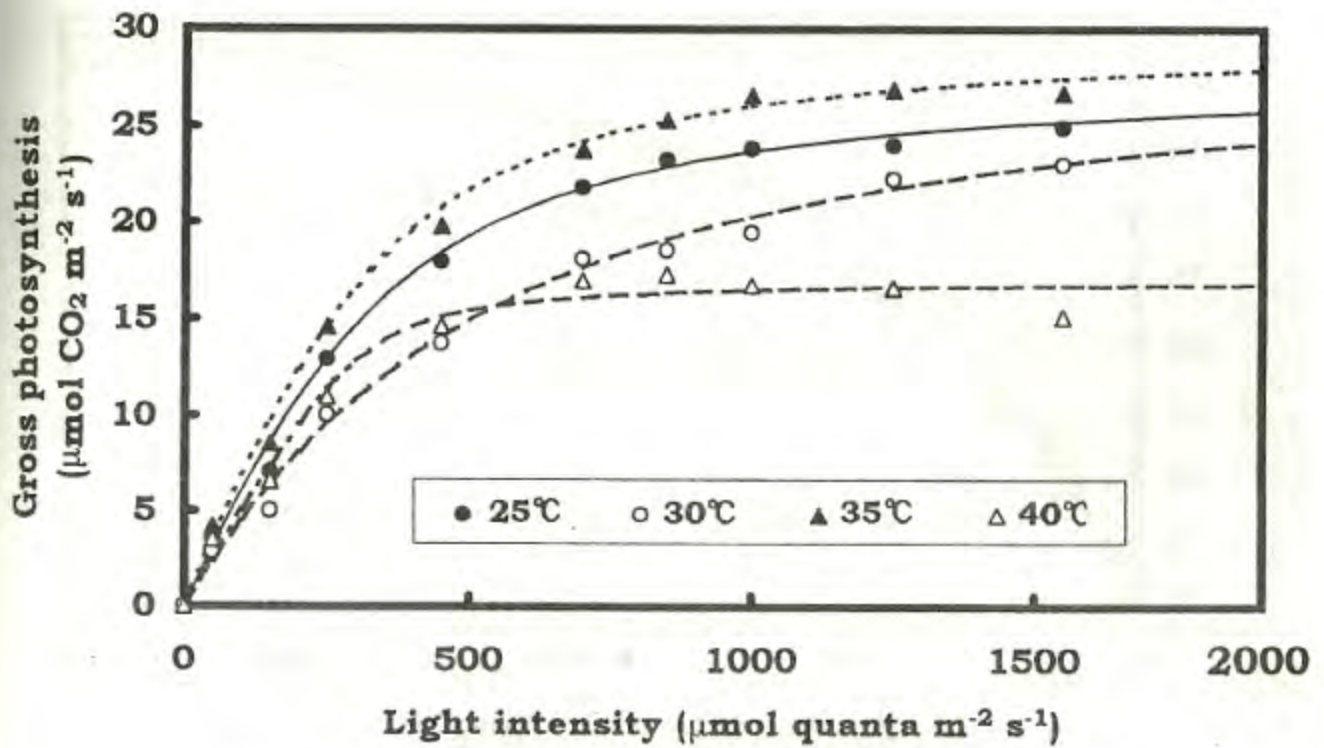


Fig 7. Gross photosynthetic light response curves at different leaf temperature fitted into non-rectangular model (leaf specimen no.4)

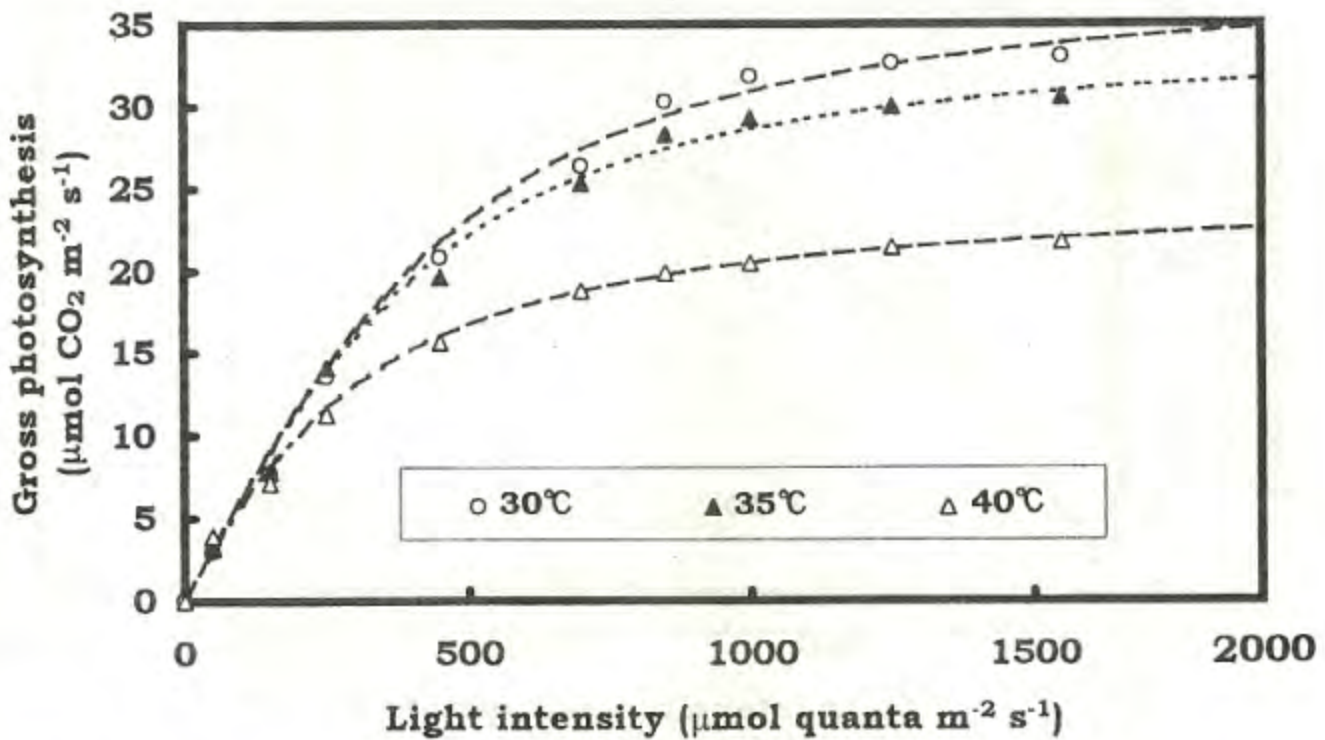


Fig.8. Gross photosynthetic light response curves at different leaf temperature fitted into non rectangular model (leaf specimen no.3)

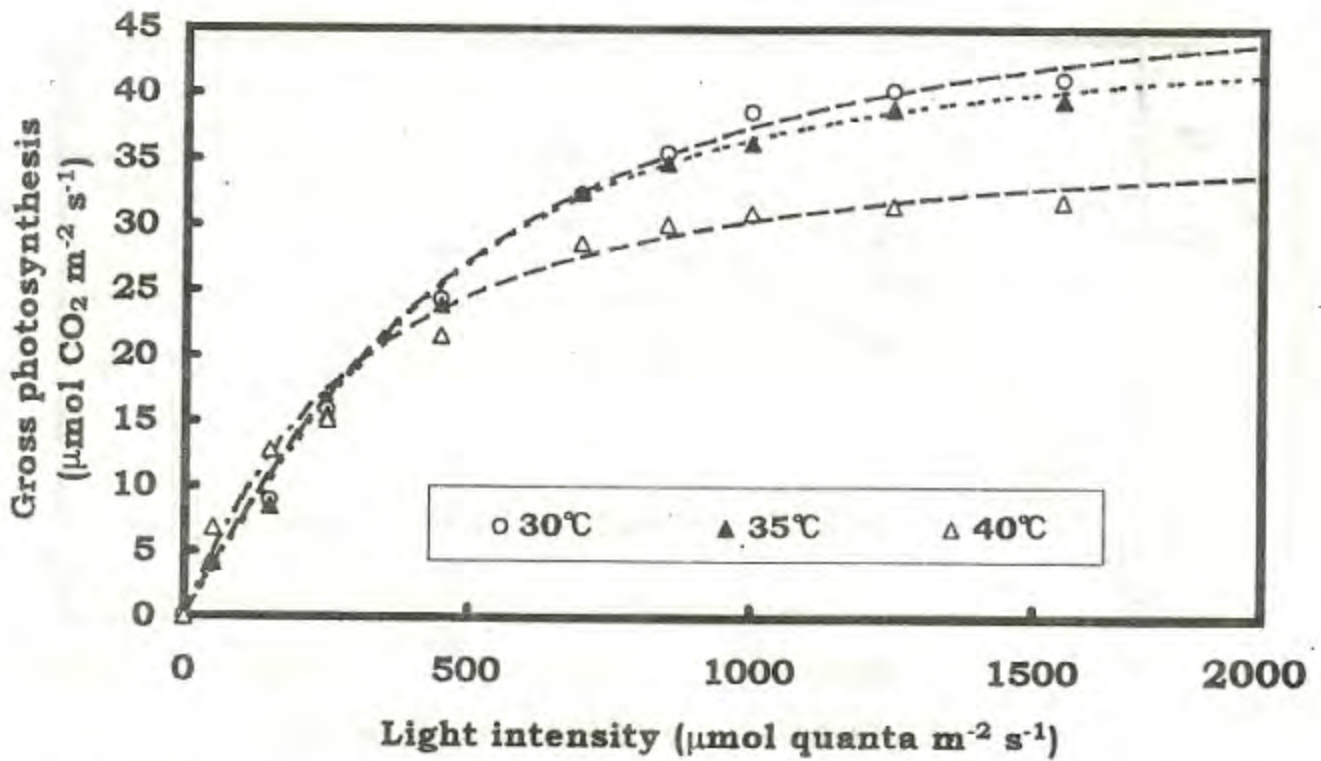


Fig 9. Gross photosynthetic light response curves at different leaf temperature fitted into non-rectangular model (leaf specimen no.2)

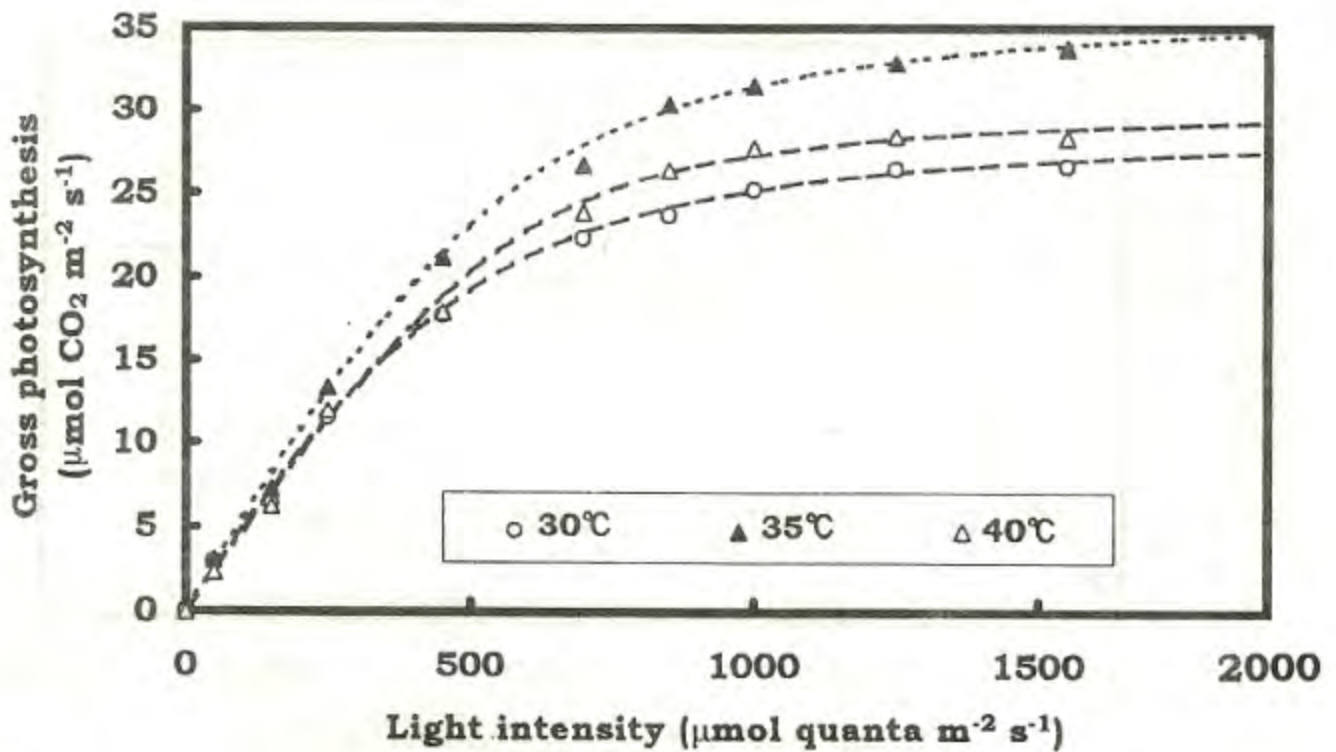


Fig. 10. Gross photosynthetic light response curves at different leaf temperature fitted into non-rectangular model (leaf specimen no.1)

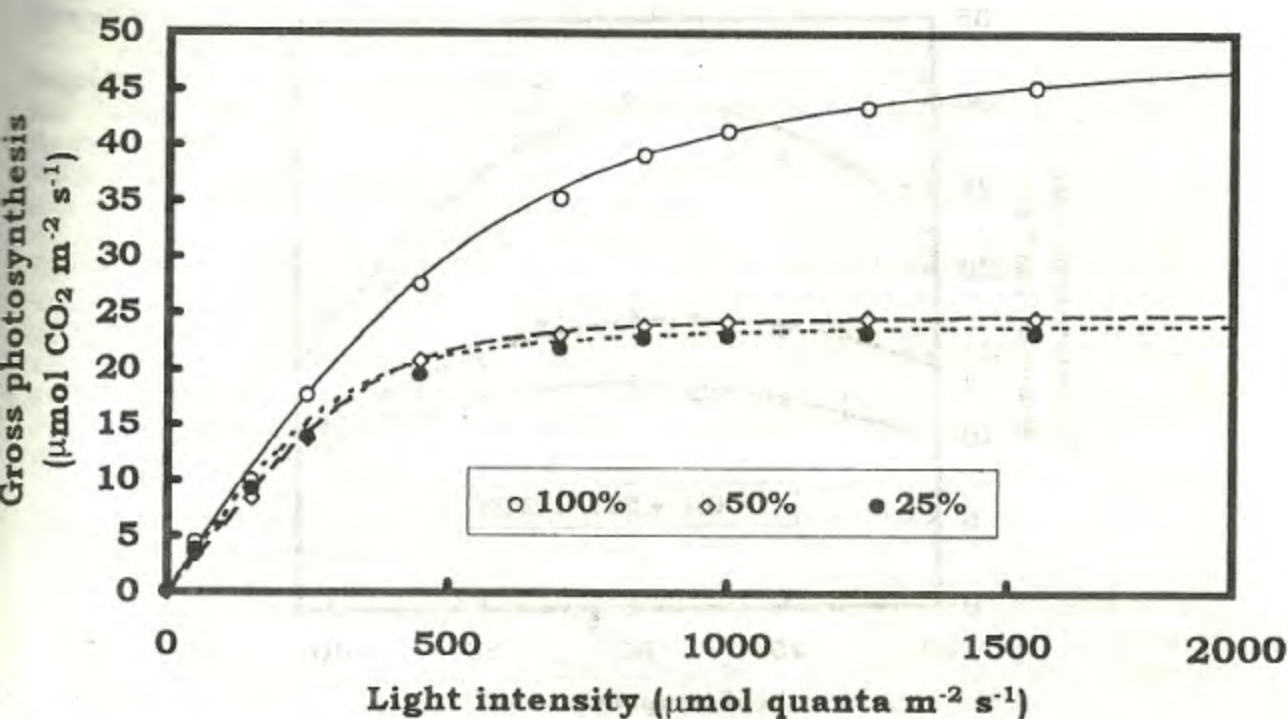


Fig 11. Gross photosynthetic light response curves of leaf grown under different irradiance at leaf temperature of 30°C.

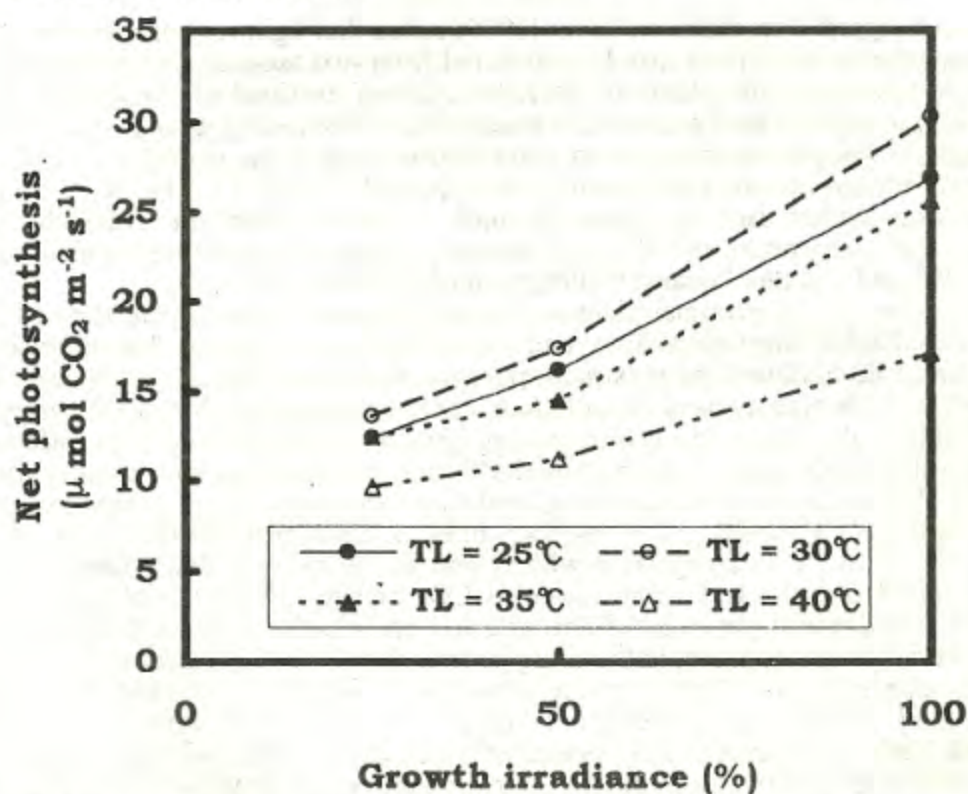


Fig. 12. Net photosynthetic rate at 1500 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$, in relation to the percentage of growth irradiance.

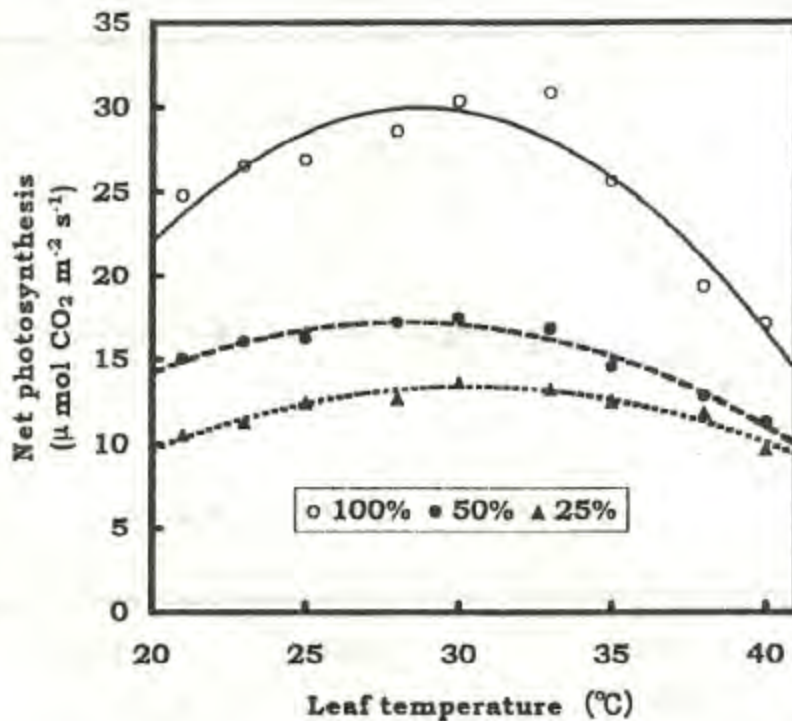


Fig. 13. Photosynthetic leaf temperature response curves of leaf grown under different irradiances at $1500 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$.

In this regard, Terashima and Saeki (1985) stated that light response curves for whole leaf photosynthesis have been mainly considered from two aspects. One is the initial slope at low light intensities, the other is the light-saturated maximal photosynthetic rate. The value of ϕ is thought to be biochemically specified and affected by among other things, leaf temperature. In the present experiments showed that initial slope varied with different leaf temperature, but no certain trend seem to be appeared (Table 1). The range of ϕ values measured were higher than ϕ values for most C_3 plants under the usual physiological condition (leaf temperature of 30°C and normal oxygen concentration) which ranged of $0.051 - 0.055 \text{ mol CO}_2 \text{ mol}^{-1} \text{ quanta}$ (Ehlinger and Björkman, 1977).

Regarding to the maximal photosynthesis, the present experiment showed that leaf temperature affected the values. Low and high leaf temperature (in this cases 25°C and 40°C) seem to be inhibited the maximum photosynthetic rate (Fig. 2, Fig. 4 until Fig. 13) and therefore soybean may have the optimum leaf temperature for photosynthesis processes. Data in Table 1 also suggested that maximum photosynthesis differed with different stage and leaf position in the plant. It seem to be that during vegetative growth, photosynthetic rate was lower than it during reproductive growth (leaf specimen ① in comparison with the others). Further, leaf position also exhibit different maximum photosynthetic rate (leaf specimen ②, ③ and ⑥ in comparison with ④ and ⑤). Relating to that matter, Acock *et al.* (1978) reported that the leaf conductance to CO_2 transfer of individual leaves from the uppermost and lower layer were differ and it were clearly associated with differences between their light environment in the canopy rather than with differences in leaf age.

The convexity of a light response curve also is important attribute. In according to Chartier *et al.* (1970), the convexity of curves are close to the ratio of r_m (mesophyll resistance) and r_x (carboxylation resistance). As regard Marshall and Biscoe (1980) formulated that Θ is the ratio of r_p to $(r_p + r_x)$, whereas r_p is physical diffusion resistance, includes the boundary layer, stomatal and mesophyll resistance, while $(1-\Theta)$ is the ratio of r_x to $(r_p + r_x)$. From this relation may summarized that varied of Θ values in this experiment

possibly due to different in biochemical level reactions as affected by different leaf temperature (Chartier *et al.*, 1970; Marshall and Biscoe, 1980).

Relating to the leaf temperature response curve, the results of present experiment suggested that soybean has the optimum leaf temperature about 30°C. According to Berry and Raison (1981), at strongly rate-limiting light intensity the response to temperature is dominated by an effect to temperature on the efficiency of light utilization. Over temperatures approaching and exceeding the temperature optimum it have assumed that the rate of CO₂ uptake is principally limited by the capacity of the primary energy conversion reactions of the chloroplast membranes. This assumption is based upon studies which show that the major enzymes of carbon metabolism are stable (and presumably fully functional) at temperature above those which resulted in complete destruction of sensitive components of the chloroplast membranes. On the other hand, as temperature is lowered below the optimum the capacities of all reactions decline. Additionally, a strong inhibition of electron transport at low temperature may also restrict CO₂ uptake, and low temperature in combination with light may result in damage to the primary photosynthetic reaction and inhibition of chlorophyll synthesis.

The difference of shape and level of leaf temperature response curves due to different growth irradiances indicated that soybean leaf photosynthesis was affected strongly by irradiances environment in which the leaf was grown. This phenomena was more clearly seen in Fig. 11 and Fig. 12. In Fig. 12 also shown that the lower the growth irradiance seem likely the lesser the effect of different leaf temperature on P_{n,max}. The difference of leaf thickness among the leaves grown under different irradiances, may responsible for different optical properties of leaf and light absorption by chloroplast and hence different photosynthetic rates (Terashima and Saeki, 1985; Terashima and Inoue, 1985).

CONCLUSION

The photosynthesis of a single leaf of soybean fitted to non-rectangular hyperbola. The values of maximal photosynthesis were strongly affected by different leaf temperature and different growth irradiance as well. Soybean leaf exhibited the leaf temperature photosynthetic response as quadratic and the optimum temperature for photosynthesis laid about 30°C.

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