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Effect of Light Quality on the Photorespiration in *Pisum sativum L.*

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완두에서 光呼吸에 미치는 光質의 影響

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ABSTRACT

Effects of blue and red light on photorespiration in the leaf disks of pea were studied. The rate of total $^{14}CO_2$ fixation was more or less higher under red light than blue light irradiation of the same quantum (94.8 $\mu Em^{-2}\cdot S^{-1}/mV$). The release of $^{14}CO_2$ by photorespiration was more stimulated under blue than red light. Among the photorespiratory intermediates, ^{14}C was more incorporated into serine under blue light than red light. However, ^{14}C was more incorporated into glycine under red light than blue light. The incorporation of ^{14}C into glycolate was very low under both light qualities, but higher under red light than blue light. Among the enzymes related to photorespiration, only glycolate oxidase was activated and/or synthesized by blue light irradiation. Moreover, more $^{14}CO_2$ was released from glycoate-1-^{14}C under blue light than red light irradiation, but $^{14}CO_2$ release from glyoxylate-1-^{14}C and glycine-1-^{14}C showed no difference by the either light qualities. These results suggest that blue light is more effective in the photorespiratory CO_2 evolution than red light. The reason is considered that glycolate is easily metabolized under blue light due to the stimulation of the glycolate oxidase activity.

INTRODUCTION

Green leaves under light produce CO_2 from photosynthetic intermediates (Tregunna *et al.*, 1964) of which the precurosr is glycolic acid (Zelitch, 1959). Glycolic acid is rapidly synthesized during photosynthesis (Kearney and Tolbert, 1962) and it can be converted into CO_2 and glycine via glyoxylic acid and serine (Tolbert, 1963; Zelitch, 1966; Kisaki and Tolbert, 1969; Tolbert, 1971). At the same time, a considerable portion of assimilated carbon is liberated in the form of CO_2 by photorespiration in the process of metabolic conversion via glycolate pathway, and this can affect the photosynthetic productivity in plants (Zelitch, 1971).

By the way, the biosynthesis of glycolate can be regulated by light quality in algae. In blue green algae (*Anacystis nidulan*) and green algae (*Chlorella vulgare* and *Chlamydomonas* sp.), glycolate is excreted into the culture media by the application of red light. But the excretion of glycolate is inhibited by blue light (Tolbert and Zill, 1956; Becker, 1968; Nelson and Tolbert, 1969, 1970; Grodzinski and Colman, 1970; Codd and

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Merrette, 1971; Colman *et al.*, 1974). In *Chlorella*, blue light inhibits the excretion of glycolate because glycolate can be easily converted into glyoxylate and glycine (Becker *et al.*, 1968). In higher plants, glycolate is much less biosynthesized by blue light (Schmid, 1969; Gnanam *et al.*, 1980). But light quality exerts no direct action on glycolate formation in isolated spinach chloroplast during photosynthesis (Poyarkova *et al.*, 1978). However, glycolate oxidase in homogenates and chloroplast suspensions from the leaves of pea grown under red or blue light is activated by blue light (Voskresenskays *et al.*, 1970). Blue light also stimulates photorespiration, as three fold increase, relative to the rete under red light in spruce (Poskuta, 1968). Above reports show the possiblity that photorespiration can be regualted by light quality in higher plants. In this paper, we undertook some experiments to prove the possibility.

MATERIALS AND METHODS

Pea (*Pisum sativum*, L., var. Hakuryu) was germinated and grown on vermiculite in Biotron at 20°C room for 15 days. The leaves on the fourth and fifth node were used for leaf disks which were the diameter of 1.3 cm. Seven disks (ca. 125 mg) were floated on water in 100 m*l* or 50 m*l* flask.

Light irradiation. In these experiments, a red filter (m = 655 nm, half-band width = 15 nm, Toshiba KL-66) or a blue filter (m = 445.5 nm, half-band width = 13.5 nm, Toshiba KL-45) was placed in front of a slide projector equipped with 1,000 W lamp and heat-absorbing water chamber. Light intensity(94.8 $\mu Em^{-2}S^{-1}/mV$) was adjusted to the bottom of flask by quantum sensor (LI-190S).

Total CO_2 fixation. Seven leaf disks were placed in 100 m*l* flask containing just enough water (1.5 m*l*) to cover the surface of the bottom of the flask. The leaf disks were placed in dark for 30 min., then they were preilluminated with blue or red light for another 30 min. with aeration of 21% O_2 and 0.03% CO_2, or 2% O_2 and 0.03% CO_2 air mixture. After the flask was sealed, $^{14}CO_2$ which evolved from $NaH^{14}CO_3$ (10 μCi) by 50% lactic acid was fixed for 5 min. $^{14}CO_2$ which was not fixed in the chamber was absorbed into 4 N NaOH solution for 1 min., then the disks were quickly taken out from the flask, washed with water and then were plunged into 80% boiling ethanol. The disks were extracted with ethanol, 3 times and the radioactivity of 1 m*l* extract solution was measured by liquid scintillation counter.

Photorespiration rate. The measurement was done by the method of Zelitch (1968). $^{14}CO_2$ (2 μCi $NaH^{14}CO_3$) was fixed for 15 min. At zero time, CO_2-free air was passed through the chamber with the flow rate of 900 m*l*/min. The released $^{14}CO_2$ was collected in 30 m*l* mixture of ethanolamine: methylcellosolve (3:1) and 0.5 m*l* aliquots were taken periodically from the absorbing solution of $^{14}CO_2$. The radioactivity of each aliquots was determined.

Determination of metabolic intermediates. 80% ethanol extracts were concentrated at 40°C with evaporator. The concentrated substance was dissolved with water and passed through the column (6 × 1 cm) of Dowex-50(H^+) and Dowex-1 x 8 (acetate form). Amino acids were eluted with 20 m*l* of 4 N NH_4OH and analyzed by paper chromatography method (Zelitch, 1959) and separated by ascending paper chromatograpy method (Zelitch, 1965). The radioactivity of each separated compounds on the paper was measured.

Determination of $^{14}CO_2$ released from Glycolate-1-^{14}C and Glycine-1-^{14}C. Seven disks of leaves were floated on 1 m*l* of water in 50 m*l* flask and preilluminated for 30 min. with blue or red light. Then, the disks were washed with 20 mM cold glycolate, glyoxylate or glycine. The water in the flask was replaced each 1 m*l* of the washed chemicals (20 mM) containing 5 μCi labelled chemicals. The $^{14}CO_2$ which was released from the leaf disks was collected into 20 m*l* mixture of ethanolamine: methylcellosolve (3:1). 0.5 m*l* of the solution was taken periodically from the absorbing solution. The radioactivity of each aliquots was measured.

Enzyme assay. Each pea leaf disks for all the enzyme assay was preilluminated with either light quality. The activities of RuBP oxygenase (EC 4.1.1.39) and glycolate oxidase (EC 1.1.3.1) were measured by oxygen electrode (YSI 53) as described by Makino *et al.* (1985) and by De Jong (1973), respectively. Phosphoglycolate phosphatase (EC 3.1.3.18) was assayed by the method of Yu *et al.* (1964). In this method, phosphorous concentration was estimated from the method of Cyrus and Subbarow (1925). Catalase (EC 1.11.1.6) was assayed by the method of Chance and Maehly (1955) with spectrophotometer by measuring the decrease of absorbance at 240 nm as H_2O_2 was

Table 1. Total $^{14}CO_2$ fixation and percentage of $^{14}CO_2$ fixed into photosynthetic lintermediates during 5 min photosynthesis

Air Mixture	Light Quality	Total $^{14}CO_2$ fixed ($\times 10^6$ cpm)	Asp.	Glu.	Ala.	Gly.	Ser.	Phe.	Glyce.	Glyco.
					(percentage of $^{14}CO_2$ fixation)					
21% O_2, 0.03% CO_2	Blue	1.096	4.7	0.7	6.0	4.4	7.4	0.6	0.6	0.1
	Red	1.312	3.0	1.3	5.9	10.1	4.3	0.3	0.3	0.3
2% O_2, 0.03% CO_2	Blue	1.169	3.0	0.3	5.5	1.9	6.2	0.4	0.3	0.3
	Red	1.360	3.7	0.5	5.9	7.6	3.8	0.5	0.1	0.2

Each value represents the average of at least three separate experiments.
Asp = Aspartate, Gly = Glutamate, Gly = Glycine, Ala = Alanaine, Ser = Serine, Phe = Phenylalanine, Glyce = Glycerate, Glyco = Glycolate.

decomposed. NADPH glyoxlate reductase (EC 1.1.1.26) and hydroxypyruvate reductase (EC 1.1.1.29) were assayed by the method of Tolbert *et al.* (1970). In case of hydroxypyruvate reductase assay, 4 mM NADH and 0.01 M hydroxypyruvate were added to the reaction mixture. In glutamte-glyoxylate reductase assay, 4 mM HADPH and 0.75 M glyoxylate were added to the reaction mixture. The two enzymes were assayed spectrophotometrically at 340 nm.

Glutamate- and serine-glyoxylate aminotransferase activity were estimated from detecting glycine-^{14}C which was formed from 20 μmole (0.02 μCi) glyoxylate-1-^{14}C (Kisaki and Tolbert, 1969). In gluoxylate aminotransferase (EC 2.6.1.4) assay and serine-glyoxylate aminotransferase (EC 2.6.1.45) assay, 20 μM L-glutamate and L-serine were added to the reaction mixture, respectively. Glycine decarboxylase (EC 2.1.2.10) activity was determined by measuring ^{14}C using the method of Peterson (1982). In this assay, 20 μmole glycine-1-^{14}C (0.1 μCi) was added to the reaction mixture in Warburg vessel. Evolved CO_2 was absorbed into KOH-soaked paper and the radioactivity was measured.

The protein concentration was estimated from the method of Lowry *et al.* (1951).

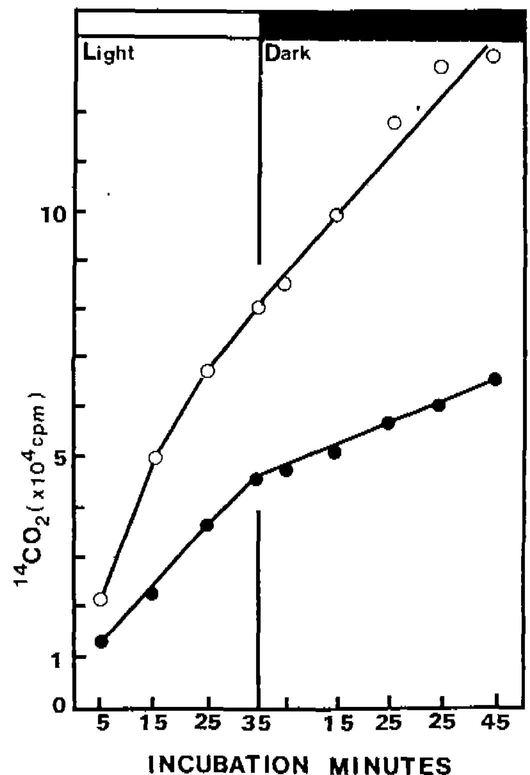

Fig. 1. $^{14}CO_2$ released in the light and dark by blue or red light irradiation in pea leaves. O–O : Blue light, ●–● : Red light

RESULTS AND DISCUSSION

Photorespiration is generally much higher in the plants which have higher light/dark ratio. The ratio is 3.0 or greater in C_3-plants, since the plant with higher rate of photorespiration evolves $^{14}CO_2$ in light condition three to five time as much as that in dark condition (Kennedy, 1976).

The ratio was 1.8 under red light and 2.8 under blue light which were low compared with that obtained in plants illuminated with white light. The amount of $^{14}CO_2$ which were evolved via photorespiraton is increased with relation to the light intensity to some extent (Decker, 1955; Tregunna *et al.*, 1966; Poskuta, 1967; Bulley *et al.*, 1969). Therefore, it may have been

Table 2. $^{14}CO_2$ released from pea leaves segments during 30 min

	Total $^{14}CO_2$ fixed ($\times 10^6$ cpm)	$^{14}CO_2$ released in light	$^{14}CO_2$ released (L/D) ($\times 10^4$ cpm)	Ratio
Blue light	3.05	5.0	2.10	2.76
Red light	3.10	3.20	1.80	1.78
Ratio (blue/red)	0.98	1.81	1.17	

The values are the average of three experiments.

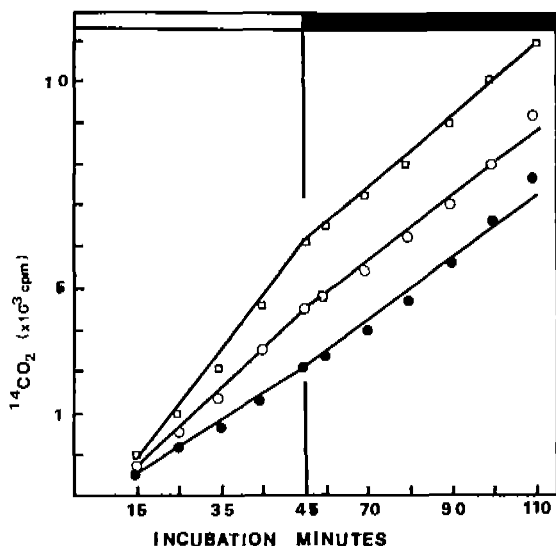

Fig. 2. $^{14}CO_2$ released from pea leaf segments floated on the solution of glycolate-1-^{14}C. □-□: Blue light, ○-○: Red light, ●-●: Dark

because of the low light intensity used in these experiments. The ratio was much higher under blue light than red light. The total amount of $^{14}CO_2$ released under blue light was about 81% higher than that under red light (Table 1). Moreover, $^{14}CO_2$ evolution was increased more rapidly under dark condition after blue light irradiation than after red light irradiation (Fig. 1).

Above results may indicate that blue light stimulates much more CO_2 evolution via photorespiration and/or dark respiration. Moreover, that blue light is effective in dark respiration (Kowallik and Gaffron, 1967; Gross and Dugger, 1969; Miyachi *et al.*, 1980) and enhances O_2 uptake (Kamiya and Miyachi, 1974; Brinkmann and Senger, 1980) is reported.

Total CO_2-fixation rate was also lower under blue light irradiation than red light irradiation (Table 2). Among the intermediates concerned with glycolate pa-

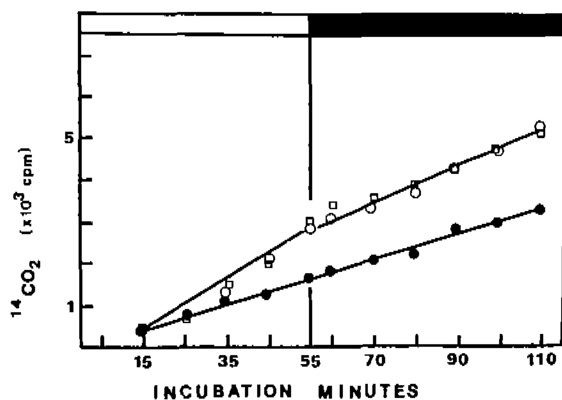

Fig. 3. $^{14}CO_2$ released from pea leaf segments floated on the solution of glyoxylate-1-^{14}C. □-□: Blue light, ○-○: Red light, ●-●: Dark

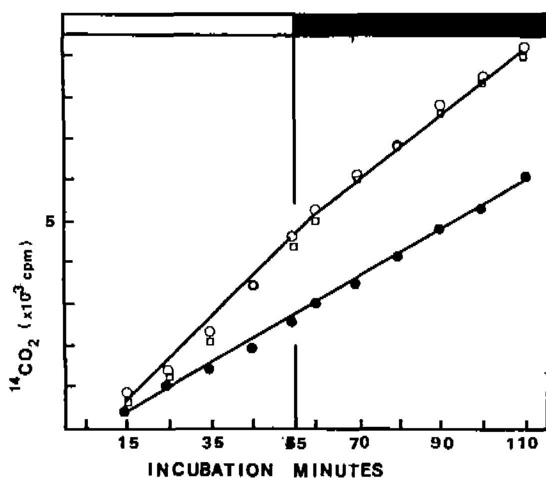

Fig. 4. $^{14}CO_2$ released from pea leaf segments floated on the solution of glycine-1-^{14}C. □-□: Blue light, ○-○: Red light, ●-●: Dark.

thway, the amount of ^{14}C incorporation into glycine was lower under blue light irradiation than red light at both 21% and 25% O_2 conditions. But the amount of

Table 3. Effect of ble light and red light on the activity of enzymes concerned with photorespiration

Time of illumination (min.)	Condition	RuBP oxygenase activity (μmole O_2/mg protein·h)	Phosphoglycolate phosphatase activity (units/mg protein·min)	Glycolate oxidase activity (μmole O_2/mg protein·h)	Catalase activity (ΔO.D./mg protein·min.)	NADPH-glyoxylate reductase activity (ΔO.D./mg protein·min.)	Glutamate-glyoxylate aminotransferase activity ($\times 10^4$ cpm/mg protein·min.)	Serine-glyoxylate aminotransferase activity ($\times 10^4$ cpm/mg protein·min.)	Glycine decarboxylase activity ($\times 10^4$ cpm/mg protein·min)	Hydroxypyruvate reductase activity (ΔO.D./mg protein·min)
60	Dark	2.97(100)	6.24(100)	22.8(100)	3.72(100)	0.68(100)	12.15(100)	8.32(100)	1.74(100)	1.47(100)
	Blue light	3.05(103)	6.58(105)	34.2(150)	3.74(101)	0.67(99)	13.04(107)	8.99(108)	1.79(103)	1.48(101)
	Red light	2.29(77)	6.27(101)	23.2(102)	3.70(99)	0.69(102)	12.75(105)	8.54(103)	1.79(103)	1.38(94)
120	Dark	3.03(100)	6.18(100)	21.4(100)	3.70(100)	0.63(100)	12.36(100)	8.61(100)	1.49(100)	1.49(100)
	Blue light	3.04(101)	6.98(113)	35.2(164)	3.61(98)	0.64(102)	13.16(106)	8.87(103)	1.48(99)	1.45(97)
	Red light	2.43(80)	6.17(100)	23.4(109)	3.69(100)	0.62(98)	12.95(105)	8.64(100)	1.59(107)	1.47(99)
180	Dark	3.00(100)	6.22(100)		3.51(100)	0.61(100)	12.06(100)	8.22(100)	1.53(100)	1.37(100)
	Blue light	3.05(102)	7.58(121)		3.40(97)	0.61(100)	13.54(113)	9.01(110)	1.47(96)	1.36(99)
	Red light	2.23(74)	6.32(102)		3.51(100)	0.60(98)	13.12(109)	8.12(99)	1.46(95)	1.35(99)
	*Dark			19.4(100)						
	*Blue light		6.01(97)	25.2(130)						
	Red light			19.7(102)						

Figures in parenthesis are percentage with reference to the dark activity. '*' indicates treatment of cycloheximide (6 μg/m*l*).

^{14}C incorporation into serine was higher blue light irradiation than red light at the same conditions. The ^{14}C incorporation into glycolate was lower under blue light than red light. These results represent that glycolate and glycine may be easily metabolized under blue light by the activation of the enzymes. Maybe light controls controls enzyme activity by two different general mechanisms. First, light controls enzyme level by interaction of synthesis and degradation. Second, light controls the activity of a pre-existing enzyme (Motagnoli, 1977; Ruyter, 1984).

The receptor of blue light is generally considered as flavin and carotenoid. But flavin is strongly accepted as the receptor because the responses to blue light in plants are similar to the absorption spectrum (460 nm, 370 nm) of flavin reactions (Shropshire, 1980; Song, 1984; Hader and Tevin, 1987). Glycolate oxidase has a coenzyme as flavin (Voskresenskaya, 1972) and is activated by blue light (Voskresenskaya and Khodzhieve, 1973; Feierabend, 1975). Among the activity of enzymes concerned on the synthesis and metabolism of glycolate, only the activity of glycolate oxidase was much increased about 50% for 60 min. and 64% for 120 min. (Table 3).

To investigate whether the increase of the activity is dependent on *de novo* synthesis or activation of the pre-existing enzyme, cycloheximide was applied. The activity under blue light (+cycloheximide) compared with that under dark condition (+cycloheximide) was increased about 30%. This incread ratio was lesser than that (64%) of cycloheximide-untreated experiments with illumination time of 120 min. (Table 3). This result suggests that the increase of the glycolate oxidase activity under blue light is dependent on both *de novo* synthesis and activation of the enzyme. Also we can suggest that $^{14}CO_2$ evolution from the metabolism of labelled compounds such as glycolate-1-^{14}C and glycine-1-^{14}C is dependent on the activity of the enzymes concerned on each steps of the metabolism, if such compounds are enough in the incubation sloution of leaf disks.

$^{14}CO_2$ evolution from the photorespiratory intermediates was also stimulated by blue or red light. But $^{14}CO_2$ which as relased from glycolate-1-^{14}C was more stimulated by the irradiation of blue light, whereas those from glyoxylate-1-^{14}C and glycine-1-^{14}C showed no difference between the two light qualities (Fig. 2, 3, 4).

Therefore, we may conclude that blue light is much more effective on photorespiration, especially by the activation and/or synthesis of glycolate oxidase.

적 요

본 연구는 완두잎 절편을 사용하여 광호흡에 미치는 청색광과 적생광의 영향을 조사연구하였다. $^{14}CO_2$고정율은 동일광양자(94.8 $\mu Em^{-2} \cdot S^{-1}/mV$)의 광을 조사할 때 청색광이 적색광보다 다소 낮았다. 그러나 광호흡으로 방출되는 $^{14}CO_2$의 양은 청색광에서 훨씬 높았다. 광호흡 중간대사산물 중 serine에 유입되는 ^{14}C의 양은 적색광보다 청색광에서 훨씬 많은 반면, glycine과 glycolate에 유입되는 ^{14}C의 양은 적색광에서 높았다.

광호흡과 관련된 효소들 중 glycolate oxidase만 청색광에 의하여 활성이 촉진되었다. 청색광은 적색광보다 glycolate-1-^{14}C에서 $^{14}CO_2$의 방출을 촉진하였지만 glyoxilate-1-^{14}C와 glycine-1-^{14}C에서 $^{14}CO_2$의 방출에는 거의 영향이 없었다.

이상의 결과들은 청색광이 적생광보다 광호흡에 의해 방출되는 CO_2를 효과적으로 촉진한다는 것을 의미한다. 그리고 청색광에 의한 CO_2 방출이 촉진되는 원인은 청색광에 의해 glycolate oxidase의 활성이 촉진되기 때문에 glycolate가 쉽게 대사되기 때문이라 사료된다.

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