The Effect of Plant Hormones and Light Quality on the Forma- tion of Chlorophyll-Protein Complexes in Maize Seedlings

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Abstract

Light qualities and three kinds of plant hormones, NAA, GA_3 and BA were treated on maize seedlings to investigate the effect on formation of the chlorophyll-protein complexes. Each three kinds of plant hormones accelerated the chlorophyll proteins formation, particularly LHCP-1 and LHCP-3, but two kinds of hormonal combinations didn't promote these proteins accumulation under sun light condition. The formation of chlorophyll proteins of LHCP-1, CPA and LHCP-3 associated with PSII was promoted under red light compared to sun light, on the contrary the formation of chlorophyll proteins was not affected by white light. Plant hormones under red light induced chlorophyll proteins formation associated with PSII at early state of chloroplast development and two kinds of hormonal combinations under red light were very effective in accumulation of chlorophyll proteins of PSII in contrast to sun light. The results obtained suggest that light may play an important role compared to plant hormones in the formation of chlorophyll proteins.

Key Words : Chlorophyll-Protein Complex, *Zea mays*, NAA, GA_3, BA, Red Light, White Light

1. INTRODUCTION

Light absorption pigments of chlorophyll have been cited mainly in three parts of CPI (chlorophyll-protein complex of PSI), LHCP (light-harvesting chlorophyll a/b protein complex) and free chlorophyll in plants (Alberte *et al.*, 1972). Nowadays these chlorophyll-protein complexes are subdivided to 8 parts by the more advanced electrophoretic tact, nomenclaturing $CPIa^1$, $CPIa^2$, CPI, $LHCP^{1,2}$, CPa, $LHCP^3$ and FC (free chlorophyll) in order of increasing mobility. The chlorophyll-protein complexes of total LHCP (LHCII) and CPa are associated with photosystem (PS) II and other chlorophyll-protein complexes cited are related to PSI

(Leong and Anderson, 1983; Leong *et al.*, 1985; Torre and Burkey, 1990). $LHCP^1$ and $LHCP^2$ presumed the reaction centre in PSII are oligomer of $LHCP^3$ on pigment composition and dissociated partly to $LHCP^3$ in electrophoretic process (Cho and Thompson, 1989). CPI is β-carotene P_{700} Chl a protein of reaction centre in PSI, and CPa related to PSII consists mainly of PSII Chl. a P_{680} complex. Torre and Burkey (1990) have proposed that CPa in electrophoretic analysis may contain a variable content of PSI light harvesting complex.

As photosynthesis implys the conversion of light energy to chemical energy, the light regimes which varied in light intensity, quality and time of irradiation are a dominant environ-

mental factor in efficient conversion of photosynthetic quantum. The composition and function of photosynthetic apparatus are sensitive to the light environment. The light quality and intensity regulate the total amounts of thylakoid membrane and chlorophyll protein of CPa and LHCII (Prioul and Reyss, 1987; Torre and Burkey, 1990) and induce the morphological and biochemical changes in chloroplast (Leong and Anderson, 1984b; Leong et al., 1985; Lechowiez et al., 1986). High light intensity causes an increase in the level of the PSII complex CPa and a decrease in the level of light-harvesting protein complexes (Torre and Burkey, 1990). The conversion of high light intensity to low causes an increase in the light-harvesting complex of PSII apoprotein, and these results induce an increase in chlorophyll a and b (Sukenik et al., 1987; Sukenik et al., 1989; Sukenik et al., 1990). Chloroplast represents significant differences in the relative amount of chlorophyll-protein complexes and in the ultrastructure of chloroplast adapted to different light quality environments (Deng et al., 1989). Recently investigations on the changes in the chloroplast composition are carried on gene level. It is proposed that either the synthesis or stability of specific plastid mRNA is influenced by different light condition (Glick et al., 1985; Melis et al., 1985). These results lead to the proposal that light quality can affect some specific chloroplast genes to induce in the levels of chloroplast emboding mRNA to encode the protein component of photopigment-protein complexes (Glick et al., 1986; Deng et al., 1989).

There are some reports that plant growth and development are influenced by the irradiation of different light quality and the treatment of plant hormones synchronously (De Greef and Fredericq, 1983; Shinkle and Briggs, 1984; Shinkle and Briggs, 1985; Owen et al., 1987; Behringer et al., 1990). Auxin is known to regulate the physiolo- gical changes induced by red light in the cell elongation of oat coleoptile and the growth of etiolated cereal seedlings (Shinkle and Briggs, 1984; Shinkle and Briggs, 1985). It is also re- ported that a reduction in GA quantity controls the physiological responses induced by red light (Behringer et al., 1990).

However, the studies on the corelation of light quality and plant hormones together in the chloroplast development are not yet enough. In this report, we examined the possibilities on the interaction between light quality and plant hormones. The present study shows the relative percentage of chlorophyll content and chlorophyll-protein complexes from maize seedlings grown in different light quality with or without plant hormones.

2. MATERIALS AND METHODS

2.1. Plant materials

The maize seeds (Zea mays L.) were soaked in running tap water for 5 hr and planted on the pot of soil, and grown in growth chamber at 28 ± 1 ℃ with 70 % humidity under dark condition for 2 days. And the seedlings were grown under 18 h of different light quality / 6 hr dark regime condition for 6 days.

2.2. Plant hormones and light treatments

The concentration of NAA (naphtaleneacetic acid), GA₃ (gibberellic acid) and BA (benzyladenine) were ascertained to 0.05 μM which was chosen for optimal concentration from the repeated preliminary experiments. The seedlings grown for 2 days under dark condition were watered and sprayed with plant hormone dilution with different wavelength of light irradiation.

Light source was a white fluorescent light and shielded with selectively light enriched acrylfilters for red and blue light. Light intensities used for growth of maize seedlings were 491 erg $cm^{-2}sec^{-1}$ for white light, 47 erg $cm^{-2}sec^{-1}$ for red light and 65 erg $cm^{-2}sec^{-1}$ for blue light with radiometer (Metrologic, 60-535, USA), and emission spectra of light sources obtained with Optical Multichannel Analyzer (EG & G PARU, 1460, USA) were shown in Fig. 1.
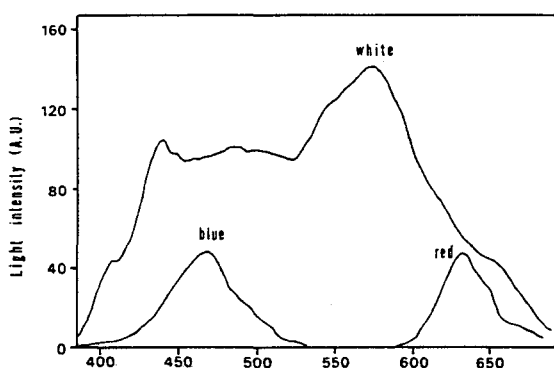

Fig. 1. Spectroradiometric scans of white, red and blue light used for growth of maize seedlings. A.U.: arbitrary unit

2.3. Chloroplast isolation

The seedlings (5 ~ 10 g) were homogenized with Waring blender in a homogenization buffer consisted of 50 mM Tricine (pH 8.0), 0.4 M sucrose, 10 mM NaCl and 5 mM $MgCl_2$. To remove cellular debris the homogenate was filtered through eight layers of miracloth, and the filtrate was centrifuged at 350 x g for 10 min. Chloroplast pellet was collected by centrifugation at 4,000 x g for 15 min, and centrifugally washed three times in distilled water, 1 mM EDTA (pH 8.0) and 50 mM Tricine (pH 8.0). The pellet was resuspended in 50 mM Tricine (pH 8.0) (Leong and Anderson, 1983). All procedures of chlorophyll isolation were

performed at 4 ℃.

2.4. Electrophoresis of chlorophyll-protein complexes

For discontinuous SDS-polyacrylamide gel electrophoresis chloroplast membranes were dissolved in the sulfactant solution containing 50 mM Tris-HCl (pH 8.0), 10 % Glycerol, 2 % Triton X-100 and 1 % SDS to give a Triton X-100/SDS/Chl weight ratio of 20:10:1 at 4 ℃. Discontinuous slab gel was consisted of a stacking gel containing 4 % acrylamide and 56 mM Tris-H_2SO_4 (pH 6.14), and a separating gel containing 8 % acrylamide and 0.22 M Tris-HCl (pH 9.35). The gel was polymerized by adding 0.1 % ammonium persulfate and 0.05 % N,N, N′,N′-tetramethylethylene-diamine (TEMED). The acrylamide/N, N′-methylene-bisacrylamide ratio was 29.2 : 0.8. The upper reservoir buffer contained 41 mM Tris-boric acid (pH 8.64) and 0.1 % SDS, and the lower reservoir buffer contained 0.43 M Tris-HCl (pH 9.35) and 0.1 % SDS modified Leong and Anderson method (1983). After the gel was pre-electrophorized at 10 mA for 30 min. samples (about 20 μg Chl) were loaded onto the gel. The amount of chlorophyll was determined with spectrophotometer (Shimadzu, UV 240, Japan) according to the method of Lichtenthaler (1987). The gel was electrophorized at 10 mA, 4 ℃ for 3 hr, and immediately the green gel was scanned at 675 nm with TLC scanner (Shimadzu, CS-930, Japan).

3. RESULTS

3.1. Relative distribution of chlorophyll-protein complexes by SDS-polyacry-lamide gel electrophoresis
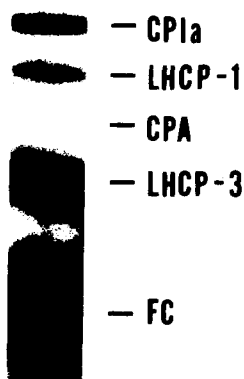
Fig. 2. Unstained SDS-polyacrylamide gel after elec-
trophoresis of chloroplast thylakoids from
Zea mays. Letters on the right-hand side
indicate the designation of chlorophyll-protein
complexes dissolved. CPIa, major PSI protein
complex; LHCP-1, oligomeric form of light-
harvesting Chl a/b protein complex; CPA,
PSII Chl a - protein complex; LHCP-3, mo-
nomeric form of light-harvesting Chl a/b
protein complex; FC, free chlorophyll.

The relative distribution of chlorophyll-protein
complexes of the thylakoids was examined by
SDS-polyacrylamide gel electrophoresis. Five
green major chlorophyll-containing bands were
obtained on gel to be nomenclatured to CPIa,
LHCP-1, CPA, LHCP-3 and FC by Cho and
Thompson (1989) (Fig.2). CPIa associated with
PSI included 49 % of total chlorophylls exclud-
ing free chlorophylls. The other chlorophyll a -
protein, CPA presumed reaction centre complex
of PSII (Leong and Anderson, 1983), included 6
% of total chlorophylls excluding free chloro-
phylls. LHCP-1 and LHCP-3 known to be main
light-harvesting Chl a/b protein complexes of
PSII included 11 % and 34 % of the chloro-
phylls, respectively.

3.2. Effect of plant hormones on the formation of chlorophyll-protein com -plexes of developing chloroplast under sun light
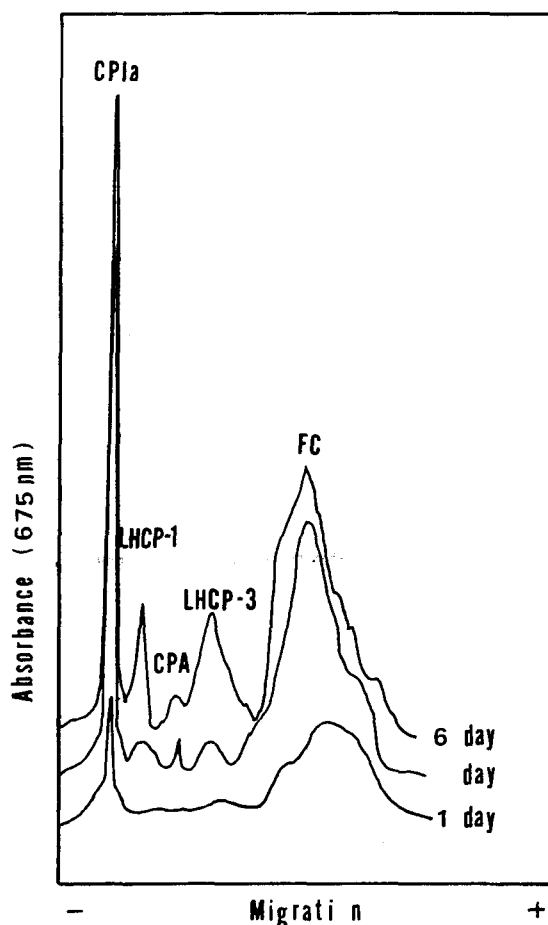

Fig. 3. Densitometric tracings of chlorophyll-protein
complexes from maize seedlings grown in
sun light for 6 days dissolved by SDS-
polyacrylamide gel electrophoresis (control)

Maize seedlings were treated with plant
hormones under sun light for 6 days and
densitometric scannings of chlorophyll-protein
complexes were shown in Figs. 3 - 6. CPIa
was appeared alone in one day grown seedlings
under sun light unrelatively to hormone treat-
ment, and the other chlorophyll-protein comple-
xes were exhibited in four to six day grown
seedlings. This fact supports that CPIa is
synthesized at more early state than the other
chlorophyll components. The formation of chlo-
rophyll-protein complexes was accelerated under
three kinds of plant hormonal treatments, re-

spectively. The accumulation of LHCP-1 and LHCP -3 of chlorophyll-protein complexes was more enhanced than that of other chlorophyll-protein complexes. In CPA synthesis, NAA and BA slightly enhanced CPA accumulation, but GA_3 was inactive to accumulate CPA. When two kinds of hormonal combinations were treated to elucidate its reciprocal effect on the formation of chlorophyll-protein complexes, they didn't affect the formation of chlorophyll-protein complexes, as compared to independent treatment (Table 1).

3.3. Effect of light quality on the formation of chlorophyll-protein complexes during chloroplast development

Maize seedlings grown in selectively enriched light quality conditions for 6 days induced the quantitative changes in chlorophyll-protein complexes (Table 2). The seedlings grown in white light showed lower level in the amount of LHCP-1, CPA and LHCP-3 compared to those grown in sun light. Although some results assert that white enriched light induces an increase in the chlorophyll proteins associated
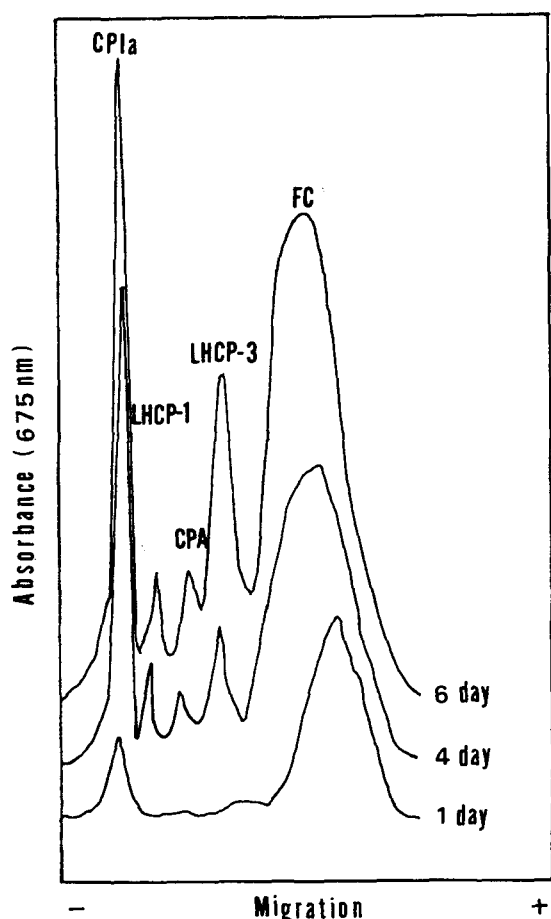

Fig. 4. Densitometric tracings of chlorophyll-protein complexes from maize seedlings treated with NAA under sun light for 6 days dissolved by SDS-polyacrylamide gel electrophoresis

Table 1. Comparison of the relative amount of chlorophyll in chlorophyll-protein complexes from maize seedlings treated with NAA+GA₃, NAA+BA and GA₃+BA under sun light

Duration of treatment	Hormone treatment	Percentage of chlorophyll in chlorophyll-proteins			
		CPIa	LHCP-1	CPA	LHCP-3
1 day	NAA+GA₃	4.18[a]	-	-	-
	NAA+BA	3.67	-	-	-
	GA₃+BA	7.05	-	-	-
4 day	NAA+GA₃	30.85	1.15	0.28	0.49
	NAA+BA	53.99	0.49	0.83	24.82
	GA₃+BA	48.62	6.05	0.39	8.08
6 day	NAA+GA₃	34.82	5.97	3.15	13.52
	NAA+BA	44.85	5.97	3.15	17.85
	GA₃+BA	29.69	7.27	3.34	11.60

a) The values are the average of three experiments

Table 2. Comparison of the relative amount of chlorophyll in chlorophyll-protein complexes from maize seedlings grown in sun light, white light and red light

Duration of irradiation	Light quality	Percentage of chlorophyll in chlorophyll-proteins			
		CPIa	LHCP-1	CPA	LHCP-3
1 day	sun	6.85[a]	-	-	-
	white	5.23	-	-	-
	red	1.48	1.53	-	-
3 day	sun	44.48	-	-	-
	white	27.01	-	-	-
	red	13.6	5.07	1.30	6.17
6 day	sun	58.49	6.98	2.45	11.06
	white	51.86	0.22	0.09	0.70
	red	35.72	9.18	3.30	9.14

a) The values are the average of three experiments

Fig. 5. Densitometric tracings of chlorophyll-protein complexes from maize sedlings treated with GA₃ under sun light for 6 days dissolved by SDS-polyacrylamide gel electrophoresis
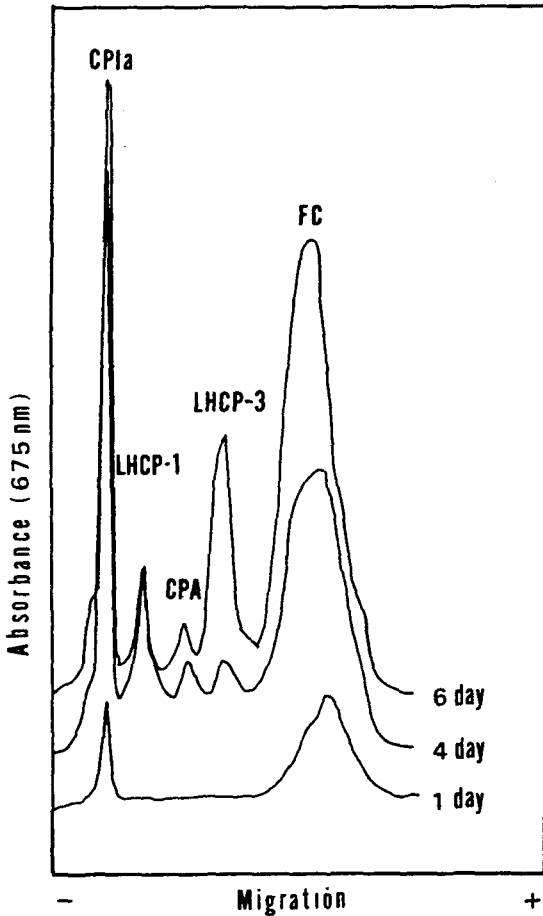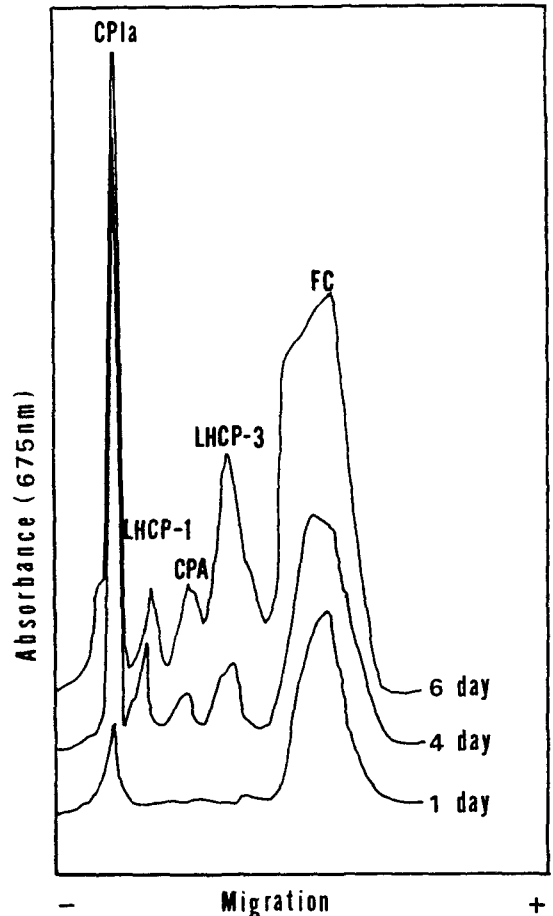

Fig. 6. Densitometric tracings of chlorophyll-protein complexes from maize seedlings treated with BA under sun light for 6 days dissolved by SDS-polyacrylamide gel electrophoresis

with PSII compared to sun light, light quality seems to cause some differences in chlorophyll proteins in some cases. Leong *et al.* (1985) represented a similar possibility that effects of light quality on the composition of thylakoid membrane was not the same for all plants. On the other hand, seedlings grown in the red light for 1 ~ 3 days had more accelerative effect on the accumulation of the chlorophyll-protein complexes related to PSII. In the seedlings obtained long irradiation of red light for 6 days, the relative CPA quantity was prominently increased comparing other chlorophyll-proteins,

but red light was ineffective in the quantitative changes of CPIa. It is ascertained that red light is available to accumulate chlorophyll proteins, and to change the composition and structure of chloroplast, because more diverse results according to the plant species is prevailing. Blue enriched light was also treated to establish the effect on the chloroplast development, bearing that the certainty needs more further experiments.

3.4. The reciprocal effect of plant hormones and light quality on the for-

mation of chlorophyll-protein com
-plexes during chloroplast develop-
ment

Table 3 shows the changes in the formation
of chlorophyll-protein complexes when maize
seedlings were treated with plant hormones
collaborated with red light for 6 days. NAA,
GA₃ and BA under red light induced an
increase in the amount of chlorophyll-protein
complexes related to PSII for 3 days. NAA was
more effective than GA₃ and BA. Plant
hormonal treatments for 6 days also caused an
increase in the chlorophyll-protein complexes,
but the relative increase for 6 days was not so
steep as compared to the increase for 3 days.
But BA-treated groups for 6 days led to
higher level in the formation of chlorophyll-
protein complexes. As shown in Table 1 and 4,
the treatments of two kinds of hormonal combi-
nations collaborated with red light at 2 days of
irradiation were remarkably effective in the
formation of chlorophyll-protein complexes asso-
ciated with PSII in contrast to those treatments
under sun light. These results were considered
that acclimation of red light was more effective
than hormonal influences on the formation of

Table 3. Comparison of the relative amount of
chlorophyll in chlorophyll-protein complex
-es from maize seedlings treated with
NAA, GA₃ and BA under red light

Duration of treatment	Hormone treatment	Percentage of chorophyll in chlorophyll-proteins			
		CPIa	LHCP-1	CPA	LHCP-3
3 day	control	13.79[a]	5.07	1.30	6.17
	NAA	38.90	4.67	2.33	9.53
	GA₃	37.55	5.14	1.09	6.82
	BA	32.46	3.74	2.07	5.54
6 day	control	35.72	9.18	3.30	9.14
	NAA	36.69	9.48	2.94	10.86
	GA₃	37.98	8.15	3.34	10.02
	BA	57.00	10.48	6.42	12.39

a) The values are the average of three experiments

Table 4. Comparison of the relative amount of
chlorophyll in chlorophyll-protein com-
plexes from maize seedlings treated with
NAA+GA₃, NAA+BA and GA₃+BA under
red light for 2 days

Hormone treatment	Percentage of chlorophyll in chlorophyll-proteins			
	CPIa	LHCP-1	CPA	LHCP-3
NAA+GA₃	27.47[a]	0.72	0.56	4.00
NAA+BA	21.30	0.52	0.56	0.83
GA₃+BA	14.38	0.91	0.83	2.10

a) The values are the average of three experiments

chlorophyll-protein complexes.

4. DISCUSSION

Maize thylakoids electrophorized with the
modified procedure of Cho and Thompson (1989)
contained five green bands resembling those
reported by others using C. reinhardtii and
higher plants (Dunahay and Staehelin, 1986;
Maroc et al.,1987), and the bands are
nomenclatured to CPIa, LHCP-1, CPA, LHCP-3
and free chlorophylls (Fig. 2). CPIa is associated
with PSI, and LHCP-1, CPA and LHCP-3 are
related to PSII, whereas Torre and Burkey
(1990) have suggested that CPA has light-
harvesting complex associated with PSI by
different electrophoretic procedure.

There are many reports on the physiological
effect of plant hormone during plant growth and
development (Pierik et al., 1988; Heyerowitz et
al., 1989; Somerville, 1989; Venis et al., 1990;
Barbier-Brygoo et al., 1990), however, little
informations are shown about the effect of plant
hormone on chloroplast development. There are
quantitative differences on the amount of
chlorophyll-protein complexes in maize seedlings
treated with plant hormones under sun light
(Figs. 3 - 6). Hormone-treated groups obtain a
large amount of chlorophyll-protein complexes,
particularly light-harvesting complexes related

to PSII compared to control. In the accumulation of CPA, NAA and BA treatments have a prominent stimulation, while GA₃ exhibits little changes compared to control. Though the physiological function of plant hormone in developing chloroplast is not yet clear, it seems likely that NAA and BA induce synergistic effect in the accumulation of chlorophyll-protein complexes, particularly that of complexes associated with PSII. These results are largely similar to results in several other reports (Huang *et al.,* 1990; Venis *et al.,* 1990). Moreover cytokinin has been known to act directly at the level of DNA and RNA in broken chloroplast (Huang *et al.,* 1990). On the other hand, two kinds of hormonal combinations are most likely not reponsible for the quantitative changes of chlorophyll-protein complexes under sun light (Table 1). From the results it is suggested that these hormonal interactions induce inhibition of the formation of chlorophyll-protein complexes, as shown in previous investigations on plant growth and differentiation (Ramasuburamanian *et al.,* 1988; Rajagopal *et al.,* 1990), but it is not yet clear whether the mutual interactions among plant hormones induce an inhibitory effect in developing chloroplast.

Light quality and intensity are shown to be sensitive to the formation of chlorophyll-protein complexes in maize seedlings. When the seedlings were grown in different light quality conditions for 6 days, the amount of LHCP-1 and CPA was increased under red light, and the amount of CPIa was decreased. Those grown in white light have a decrease in total chlorophyll-protein complexes compared to those grown in sun light condition. Moreover there are various changes in the amount of chlorophyll-protein complexes associated with PSII in the seedlings grown in red light for 3 days

compared to those grown in sun light and white light for same period (Table 2). The results agree with the observations that spinach seedlings grown in red light have higher amount of chlorophyll-protein complexes related to PSII and lower amount of chlorophyll-protein complexes associated with PSI than those grown in white and yellow light (Deng *et al.,* 1989). Other plant species also show the similar changes in chlorophyll-protein complexes (Melis *et al.,* 1984; Glick *et al.,* 1986). Though there are some reports that pea seedlings grown in white light have higher amount of chlorophyll-proteins associated with PSII than those grown in sun light (Leong and Anderson, 1983), white light is ineffective in the formation of chlorophyll- protein complexes associated with PSII compar- ed to sun light. Therefore, it is suggested that the effect of light quality and light intensity may induce some different results on the for- mation of chlorophyll-protein complexes during chloroplast development.

In the treatment of plant hormones collaborated with red light for 3 – 6 days, plant hormonal treatments cause enrichment in the amount of LHCP-1 and LHCP-3, particularly BA remarkably enhances the amount of total chlorophyll-protein complexes in developing chloroplast of maize (Table 3). Plant hormone treatments under red light seem to accelerate the formation of light-harvesting complex associated with PSII during early state of chloroplast development. The interactions between plant hormones and light quality are seemed to be consistent with some reports on plant growth and differentiation (Shinkle and Briggs, 1985; Owen *et al.,* 1987; Reid, 1988; Huang *et al.,* 1990; Martinez-Garcia and Garcia-Martinez, 1992). Also the treatments of two kinds of hormonal combinations under red light have synergistic effect in the formation of chloro-

phyll-protein complexes associated with PSII during early state of chloroplast develop- ment in contrast to the treatments of two kinds of hormonal combinations under sun light (Table 4). From these results it is insufficient to express a foregoing discussion about reciprocal effect of plant hormones and light, but light seems to be more important factor to lead some physiological derivations than hormones. There- fore, it is considered that the effect of red light is more profound than hormonal effect on the formation of chlorophyll-protein complexes, and hormonal inhibition by mutual interaction may be controlled by red light during more early state of chloroplast development. It will be great interest to establish the interaction between plant hormones and light quality in gene level during chloroplast development, because it is suggested that chloroplast development in red light or some enriched light quality undergoes significantly morphological adjustment of thyla- koid membrane complexes, and these functional and structural changes are attributed by the plastid mRNA encoding photosynthetic compo- nents.

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옥수수 유식물의 엽록소-단백질 복합체 형성에 미치는 식물호르몬 및 광선의 효과

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자연광 및 여러 파장의 광선과 NAA, GA₃ BA 등의 식물호르몬을 옥수수 유식물에 처리하여 엽록소-단백질 복합체 형성에 미치는 효과를 조사하였다. 자연광하에서 3 종류의 호르몬 처리는 전체적으로 엽록소-단백질 복합체, 특히 LHCP-1과 LHCP-3의 형성을 촉진하였으나, 2 종류의 호르몬 조합은 엽록소-단백질 형성에 효과적이지 못하였다. LHCP-1, CPA 및 LHCP-3 등의 광계 II 관련 엽록소 형성에 있어서 백색광은 자연광에 비하여 효과가 적었으나 적색광은 효과적이었다. 적색광하에서 식물호르몬의 단독처리는 엽록체 발달 초기에 광계 II의 엽록소-단백질의 양적 증가를 유도하였다. 한편, 적색광하에서 2 종류의 호르몬 조합 처리도 자연광하에서의 처리와는 대조적으로 광계 II의 엽록소-단백질 형성에 매우 효과적이었다. 이와 같은 결과는 광선처리의 효과가 호르몬처리 효과보다 엽록소-단백질 복합체 형성에 중요한 인자로 작용한다는 것을 시사해 준다.