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Changes in Chloroplast Ultrastructure and Thylakoid Membrane Proteins by High Light in Ginseng Leaves

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Ultrastructural changes in *Panax ginseng* C. A. Meyer mesophyll chloroplasts and variation of thylakoid membrane proteins in responce to the light intensity were studied in leaves of two-y-old plants exposed to two different light intensities under field conditions. The leaves were allowed to function for three months after emergence under two contrasting light conditions. The ginseng chloroplasts of 5% light were filled with highly stacked grana of condensely arrayed thylakoids, so that the stroma space was hardly observed. In contrast, chloroplasts from leaves at 100% sunlight had fewer thylakoid membranes and smaller grana stacks. The number of osmiophilic globules increased. Total Chl content and Chl b content were lower at 100% sunlight than 5% sunlight. The thylakoid membrane proteins in the leaves grown at 100% sunlight showed lower CPIa, LHCII* and CP29 than those with 5% sunlight. This effect was most obvious for LHCII*. Polypeptides showed major bands at 90, 64, 29-30, 22 and 14 kD, and minor bands at 59, 58, 54, 52, 49, 46, 44, 35, 23, 21 and 18-19 kD. All these bands were lower in intensity in the leaves exposed to 100% sunlight. Moreover, the bands at 58-59, 46-47 and 23 kD disappeared.

Keywords: LHCII, thylakoid membrane, CP-complex, osmiophilic globule

Panax ginseng C. A. Meyer is a perennial herb in the family Araliaceae. The plant is cultivated for medicinal purposes under shaded conditions. While various factors affect the growth of ginseng such as light intensity, temperature, soil water content, etc., light intensity is the most important factor that has been investigated most extensively. Root growth of ginseng decreases under light intensities below 3000 luces due to slow assimilation. However, if the light intensity is too high, chlorophyll is damaged and this also leads to a decrease in the photosynthetic activity (Cheon, 1989). Thus, the light intensity and quality are important growth factors that affect the photosynthesis rate directly and also indirectly through causing changes in the granum structure, the composition of chlorophyll-protein complexes and the composition of the thylakoid membrane proteins (Degreef *et al.*, 1971; Bushmann *et al.*, 1978).

Previous work on the influence of the light intensity on the chloroplast structure has been carried out mostly for sun plants. These studies suggest that high light intensity causes chloroplast structural changes. These include dilation of the thylakoid membrane, decrease in the number and size of starch grains and increase in the number of osmiophilic globules within the chloroplast (Hernandez-Gil and Schaedle, 1973; Coloquhoun *et al.*, 1975).

It is generally accepted that high light influences the structure of CP-complex and the chlorophyll content of leaves (De la Torre *et al.*, 1990). The leaf senescence induced by high light intensity results in a decrease in the concentration of proteins that are involved in photosynthesis, such as ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco), light harvesting chl-protein complex (LHCP), cyt b/f com-

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plex and ATP synthetase (Leong and Anderson, 1984; De la Torre and Burkey, 1990; Mae *et al.*, 1993). In particular, the decomposition of the CP-complex coincides with chlorophyll decomposition, which can be identified by the changes in leaf colour from green to yellow (Hilditch *et al.*, 1989). Park (1980) has reported that Chl content decreases while Chl a/b ratio increases when ginseng leaves are exposed to high light intensity. Yang *et al.* (1987) attributed the ginseng leaf-tissue damage, that occurs during leaf-exposure to direct sunlight over a long period, to the photooxidation of chlorophyll.

Previous studies on the effects of high light on the ultrastructure of chloroplasts are mostly focused on leaf senescence with sun plants (Hernandez-Gil and Schaedle, 1973; Coloquhoun *et al.*, 1975; Lee *et al.*, 1982). Very few studies have been performed on the effect of high light intensity on the chloroplast structure and the thylakoid membrane proteins in shade plants leaves, and no such work on ginseng has been reported.

In the present study, ginseng leaves of plants grown in the field at 5% sunlight (5000-7000 luces) exposure were compared with those grown at 100% sunlight (12,000-15,000 luces). Thus the effect of high light intensity on PSII has been investigated from the viewpoint of chloroplast ultrastructure and the thylakoid membrane proteins.

MATERIALS AND METHODS

Materials

Two-year old ginseng (*Panax ginseng* C. A. Meyer) plants were allowed to function for 3 months after emergence at 5% (5000-7000 luces) and 100% (12,000-15,000 luces) sunlight intensities under field condition at the Korea Ginseng and Tobacco Reserch Institute (Fig. 1A, B).

Ultrastructure

Leaves were dissected under fixative into 1 mm^2 pieces. Tissue pieces were fixed in 4% paraformaldehyde-5% glutaraldehyde in sodium phosphate buffer (25 mM, pH 7.1) for 2 h, rinsed three times in same buffer and post fixated in 2% OsO_4 for 1.5 h. The tissue blocks were dehydrated in a graded series of ethanol and embedded in an Epon-Araldite mixture.

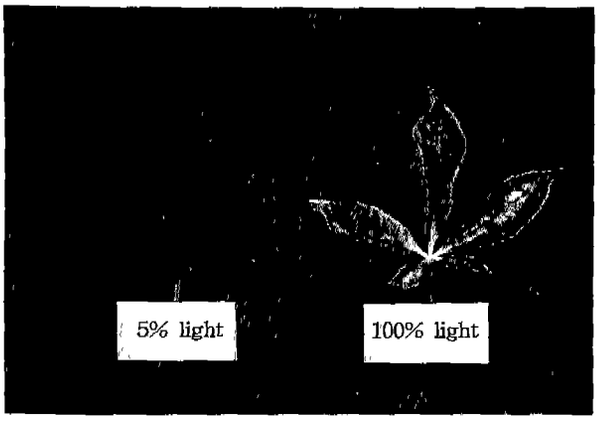

Fig. 1. Two-y-old ginseng leaves grown for 3 months after the emergence: A, under normal exposure (5% sunlight); B, under full sunlight exposure (100%).

Silver sections were cut with an LKB-V ultramicrotome and collected on collodion coated copper grids, and then stained with uranyl acetate and lead citrate. Sections were examined with JEOL JEM 100 CX-I transmission electron microscope at 80 kV.

Isolation of thylakoid membranes

Ginseng leaves (2 g) were homogenized in a chilled porcelain mortar with 30 mL medium containing 0.33 M sorbitol, 2 mM EDTA, 1 mM $MgCl_2$, 1 mM $Na_4P_2O_7$ and 50 mM Hepes-NaOH (pH 6.9). Ribulose 1,5-bisphosphate carboxylase and other soluble proteins were removed with three 10 mL washes with 10 mM $Na_2P_2O_7$-HCl (pH 7.4), followed by three washes with 0.3 M sucrose, 2 mM tricine (pH 7.0) to remove coupling factor.

Isolation of Chl-protein complexes

Undenaturated chlorophyll protein complexes were resolved by a modification of Camm and Green's method (1980) with the addition of the protease inhibitors, 5 mM ε-aminocaproic acid and 1 mM benzamidine-HCl to all buffers. Isolated thylakoid membranes were washed twice with 2 mM Tris-maleate buffer (pH 6.8) and then suspended in 300 mM octylglucoside in the same buffer to give a detergent (octylglucoside)/Chl ratio of 20 : 1 and stirred for 5 min at 4℃. The solution was then diluted with 2 vol. 40% glycerol in Tris-maleate (pH 8.0).

Electrophoresis

Nonsolubilized material was removed by centrifugation at 10,000 *g* for 30 min. The supernatant was loaded directly on to SDS-polyacrylamide gels (10% separating, 4% stacking) Laemmli (1970) and electrophoresis was done at 20 mA for 4 h in the dark at 4℃.

Spectroscophy

Gels were stained with coomassie blue and then destained. Spectra of CP-complexes were determined using Beckman DU-7 spectrophotometer and the stained gels were scanned with LKB laser densitometer.

Chl determination

Chl content and the Chl a/b ratio of fresh leaf discs were determined by extraction of pigment with 80% acetone for 1 wk according to the method of Arnon (1949). Chl concentration of Chl-protein complexes was determined in 80% acetone using a Shimatzu UV-190 spectrophotometer (Arnon, 1949).

RESULTS

Changes in the chloroplast ultrastructure

The ginseng leaves grown under 5% sunlight (Fig. 1A) were dark green color. In contrast, leaves grown under 100% sunlight (Fig. 1B) were small and yellowish green color. The surface of these leaves was rough compared with the leaves grown under 5% sunlight.

Chloroplast ultrastructure of ginseng leaves at 5% sunlight was characteristic of that of a typical shade plant. Almost the entire vol. of the chloroplast was occupied by large well developed grana stacks, and thus there was a drastic loss in the stroma vol. compared with sun plants (Fig. 2). Some chloroplasts contained many large starch grains, and except for these starch grains, the chloroplast was filled with well developed grana stacks (Fig. 3). Moreover, the chloroplast contained few, small osmiophilic globules which might be lipid bodies (Figs. 2 and 3).

In the ginseng leaves exposed to 100% sunlight, the thylakoids decreased dramatically and the stroma vol. increased (Fig. 5). The starch grains disappeared or the number decreased. Both the size and the number of osmiophilic globules increased (Figs. 4 and 5). Some of the thylakoids were degraded and faded (Fig. 4).

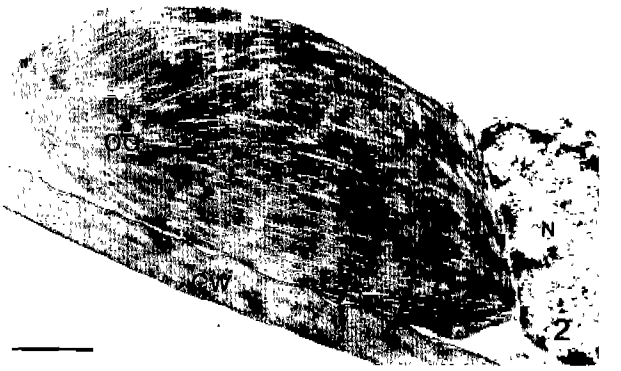

Fig. 2. Electron micrograph of mesophyll chloroplast from 5% sunlight grown plants showing extended grana stacks, high membrane density and decreased stroma vol. Bar=1 μm.

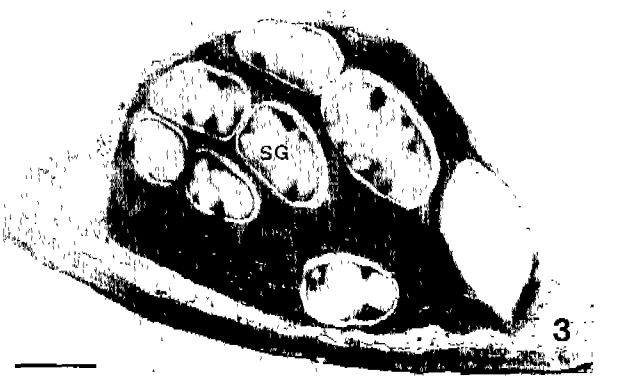

Fig. 3. Electron micrograph of mesophyll chloroplast obtained from 5% sunlight shows the grana stacks and large starch grains. Bar=1 μm.

Changes in the thylakoid membrane proteins

Six CP-complex bands were obtained when the thylakoid membrane proteins from the ginseng leaves shown in Fig. 1A and B were separated by DSD-PAGE under non-denaturing conditions. According to the nomenclature by Camm and Green (1980), these complexes can be classified as CPIa (reaction center of PSI), CPI (P_{700}-chl a protein of PSI), LHCII* (oligomeric light harvesting chlorophyll protein complex of PSII), CPa (reaction center of PSII),

Fig. 4. Electron micrograph of mesophyll chloroplast obtained from plants grown in 100% sunlight shows numerous osmiophilic globules and indication of thylakoids lysis (arrow). Bar=1 μm.

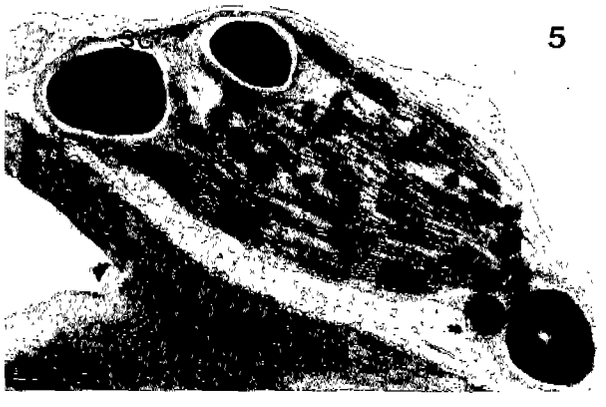

Fig. 5. Electron micrograph of mesophyll chloroplast obtained from 100% sunlight shows that grana stacks have decreased while the osmiophilic globules have increased. Bar=1 μm.

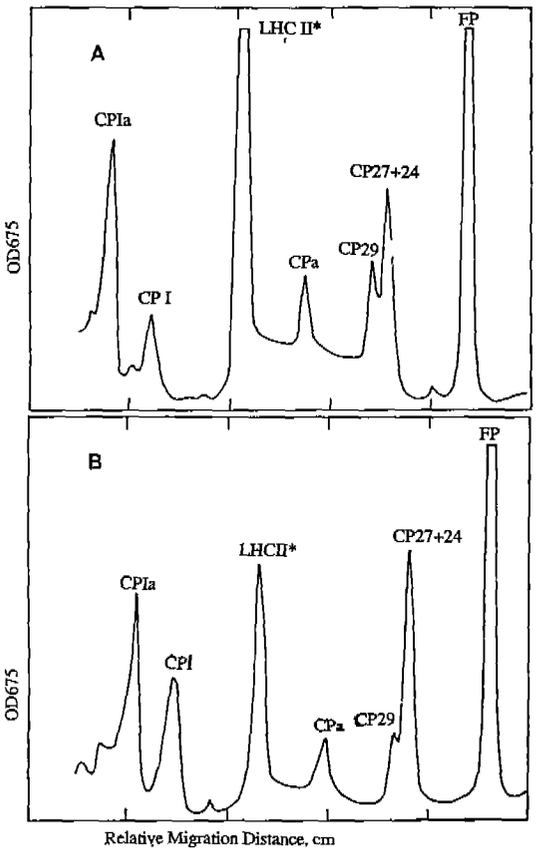

Fig. 6. Densitometric scans of CP-complex separated by mild SDS-PAGE of octylglucosidc-solubilized thylakoid membranes for 2-y-old ginseng leaves grown for 3 months after emergence: A, under 5% sunlight; B, under 100% sunlight exposure.

CP29, CP27 and CP24 (Fig. 6A, B). Leaves from both 5 and 100% sunlight condition gave the same green bands which were separated into identical molecular weight proteins. Gel scanning at 675 nm indicated that the exposure of the ginseng leaves to 100% sunlight led to significant decreases in the CP-complex band intensities for CPIa, LHCII*, CPa and CP29 (Fig. 6B). The band intensity change for LHCII* was greatest.

SDS-PAGE of the leaf sample obtained under 5% light condition gave major polypeptide bands estimated to be 89, 65, 29-30, 22 and 14 kD, and minor bands at 59, 58, 54, 52, 49, 46, 44, 35, 23, 21 and 18-19 kD (Fig. 7A, B). However, the bands at 58-59 kD, 46-47 kD and 23 kD polypeptides were absent in the SDS-PAGE of the 100% light-exposed sample (Fig. 7B).

Changes in the Chl content and Chl a/b ratio

Compared with the ginseng leaves grown with 5% sunlight, the leaf sample obtained with 100% sunlight showed low concentration of both Chl a and Chl b. However, the Chl a/b ratio was higher in the case of 100% sunlight-exposed leaves than the leaves grown at 5% sunlight (Table 1).

DISCUSSION

When plants are exposed to different light irradiance, acclimation of their photosynthetic systems to the new environment follows in various ways. The Chl a/b ratio differs according to light intensity. The electron transport capacity and the proportion of

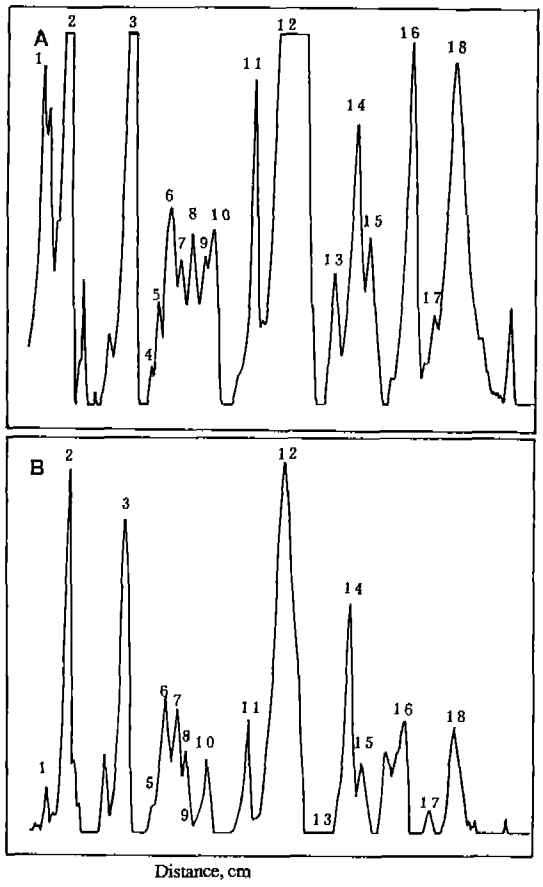

Fig. 7. Thylakoid membrane polypeptides separated by SDS-PAGE of SDS-solubilized thylakoid membranes from 2-y-old ginseng leaves grown for 3 months after emergence: A, under normal exposure (5% sunlight); B, under full sunlight exposure (100%). The peaks are identified as follows: 1, 99 kD; 2, 89 kD; 3, 65 kD; 4, 59 kD; 5, 58 kD; 6, 54-55 kD; 7, 53 kD; 8, 49-50 kD; 9, 46-47 kD; 10, 44-45 kD; 11, 35-36 kD; 12, 29-30 kD; 13, 23 kD; 14, 22 kD; 15, 21 kD; 16, 18 kD; 17, 16 kD; 18, 14 kD.

Table 1. Chl a, b content and Chl a/b ratio of 2-y-old ginseng leaves grown under normal (5% sunlight) and full sunlight (100%) exposure for 3 months after emergence, respectively

Light intensity (%)	Chl a[a]	Chl b[a]	Total Chl[a]	Chl a/b
5	2.50± 0.05	0.91± 0.01	3.41± 0.06	2.74± 0.04
100	1.33± 0.16	0.45± 0.05	1.78± 0.20	2.99± 0.06

[a]mg/g fr wt.

chloroplast vol. occupied by the thylakoids and stroma respectively also differ. The content of thylakoid membrane proteins, particularly LHCII is closely related to the light irradiance (Melis and Harvey, 1981; Hoyer-Hansen *et al.*, 1988).

High light intensity produces distinctly different effects on the ultrastructure and function of chloroplast. The chloroplasts are sensitive to the light irradiance and the symptoms of high light irradiance to plant leaves are usually expressed first in the chloroplasts. The color of the leaf changes from green to yellow. Changes in the chloroplast ultrastructure include loss of starch grains, disappearance of plastid ribosomes, dilation of thylakoids and loss of the chloroplast envelope (Hernandez-Gil and Schaedle, 1973; Coloquhoun *et al.*, 1975).

The appearance of large osmiophilic globules within chloroplasts is the most conspicuous indicator of the changes due to high-light irradiance (Harris and Arnott, 1973; Simpson and Lee, 1975). Although much attention has been paid to the formation of the osmiophilic globules, the detailed mechanism has not been clarified. Harris and Arnott (1973) have suggested that the osmiophilic globules are plastosomes with suborganelles which are released into the cytoplasm. Thi and Silva (1977) believed that the osmiophilic globule is composed of protein or lipid since the globule is formed from chloroplasts at the last stage of degradation and reacts with lipase, protease and phospholipase. It has also been reported that the color change taking place during the ripening of fruit or seed occurs because the chloroplast is transformed into a chromoplast due to a dramatic increase in the number of osmiophlic globules and degradation of the lamella structure in the grana (Thomson, 1966; Kim and Kim, 1984). Thomson (1966) believed a more direct linkage between the formation of osmiophilic globules through the breakdown of lipoprotein membrane. Ben-David *et al.* (1983) have shown that the lipid composition in the thylakoid membrane changes along with the morphological changes in chloroplasts, which bring about a decrease in the rate of photosynthetic activity. The present work shows a very conspicuous increase in the number of osmiophilic globules along with the granal lysis due to high light irradiance to ginseng leaves (Figs. 4 and 5). Thus, it is a reasonable assumption that the increase of osmioplic globules is closely related to the granal lysis and the osmiophilic substances in the globules may come from the breakdown of the grana.

Proteins of thylakoid membrane can be classified into four groups. PSI proteins such as CPI and

LHCI belong to the first group. PSII proteins such as LHCII, CP47, CP43, CP29, CP27 and CP24 belong to the second, and these participate in the absorption and transfer of the proton energy to the phtosynthetic reaction centers (P_{700}, P_{680}). Cyt b_6/f complex is included in the third group. This complex operates electron transfer from H_2O to NADP, between PSI and PSII. ATP synthetase belongs to the last group (Bassi *et al.*, 1987; Olive and Vallon, 1991). In contrast to sun plant, shade plant leaves have a low capacity not only for photosynthetic electron transport but also for the photoprotection through the dissipation of excess light. If shade plants are exposed to excessively high light intensity above their capacity, a decrease in the efficiency of photosynthetic energy conversion takes place as a means of photoprotection prior to the photoinhibition. It is generally accepted that photoinhibition adversly affects the function of PSII and it is manifested as lowered rates of electron transport and oxygen evolution. The photoinhibition can results not only from some form of damage to PSII but also from an increase in thermal energy dissipation. The PSII damage can result in inactivation of the photochemical reaction center of PSII or decreased transfer of the excitation energy to PSII (Demmig-Adams and Adams, 1992).

In the present work, high light irradiance of ginseng leaves resulted in a decrease of the CP-complexes. In particular, there was a conspicuous decrease of LHCII. SDS-PAGE of the thylakoid membrane proteins also showed a decrease in the polypeptides concentration due to high light intensity. Along with the decrease of CP-complexes, the decrease of these light harvesting polypeptides indicates a significant loss in the photosynthesic efficiency since such a decrease of light harvesting proteins in PSII can reduce the efficiency of transfer in PSII through photoinhibition. The disappearance of 58-59, 46-47 and 23 kD peaks is particularly noteworthy. Since the 58-59 kD polypeptide is known as CF_1 protein (Olive and Vallon, 1991), ATP synthesis is believed to be affected by irradiation with the high light intensity. The 23 kD polypeptide is known to participate in oxygen evolution (de Vitry *et al.*, 1989), and the disappearance seems to be affected in the oxygen evolution function. The function of 46-47 kD polypeptide has not yet been clarified and then requires further work. As shown in Table 1, the ginseng leaves grown in 100% sunlight irradiance contained less Chl than the leaves grown in 5% sunlight. The Chl a/b ratio of the sample obtained with high light irradiance was higher. This results indicate the total Chl content decreased due to the high light irradiance, and Chl b is more easily damaged by the light than Chl a, in good agreement with the previous result obtained by Park (1980). Since Chl b is mainly distributed in LHCII (Di Paolo *et al.*, 1990) the decrease of Chl b seems to be closely related to a decrease of LHCII in thylakoid membrane. Moreover, since LHCII is distributed mainly in grana, the decrease of LHCII is closely related with the granal lysis in ginseng leaves.

From the above results, it is believed that the exposure of a shade plant ginseng to strong sunlight leads to a process resulting in a loss of a light harvesting protein LHCII in PSII, and thus the strong light intensity affects most remarkably PSII in the photosynthetic system. These results agree with a significant decrease in the activity of PSII reaction center when shade plants are exposed to high light (Demmig-Adams and Adams, 1992).

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強光에 의한 人蔘 잎의 葉綠體 微細構造 및 틸라코이드 膜蛋白質의 變化

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적 요

상대광량 5%와 100% 광노출 조건에서 재배한 인삼(*Panax ginseng* C. A. Meyer) 잎을 대상으로 광도 변화에 의한 엽록체의 미세구조와 틸라코이드 막 단백질의 변화상을 연구하였다. 인삼 잎은 출엽 후 두 광조건하에서 3개월간 재배 포장에서 생육한 후 실험 재료로 사용하였다. 5% 광노출 조건의 인삼 잎의 미세구조는 틸라코이드 막들이 잘 발달하여 많은 grana stack을 이루고 있었으나 100% 광노출 조건하에서는 grana stack의 현저한 감소와 지질 계통의 물질이 축적된 호 오스뮴성 소구체들이 증가하였다. 또한 100% 광노출 조건하에서 인삼 잎의 엽록소 a, b 함량이 모두 낮았으며 엽록소 a/b 비율이 5% 광노출 조건보다 높았다. 틸라코이드 막의 단백질을 SDS-PAGE하였을 때 100% 광노출 조건에서 LHCII*의 현저한 감소가 있었다. 또한 polypeptide 조성을 분석한 결과 major band로 90, 64, 29-30, 22, 14 kD과 minor band로 59, 58, 54, 52, 49, 46, 44, 35, 23, 21, 18-19 kD이 관찰되었다. 특히 100% 광노출 조건하에서는 모든 polypeptide의 농도가 감소하였으며 58-59, 46-47, 23 kD은 소실되었다.

주요어: LHCII, 틸라코이드막, CP 복합체, 오스뮴성 소구체

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