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Effects of Spermine on Changes in Chlorophyll-Protein Complexes and Plastid Membrane Proteins of Mung Bean Cotyledons during Greening

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Abstract

Developmental changes of chlorophyll-protein complexes (CPs) and plastid membrane proteins in greening mung bean cotyledons and the effect of spermine thereon were examined by SDS-polyacrylamide gel electrophoresis. The changes in the amounts of CPs became larger with the progress of greening and light-harvesting chlorophyll a/b protein (LHCP) was the main CP in the early greening stage up to 48 h. As the greening proceeded, chlorophyll-protein of the photosystem I (CPI) accumulated. Application of spermine were effective in accumulating CPs of the thylakoid membrane in the early phase of greening. In the profiles of the plastid membrane proteins, quantitative and qualitative changes were observed with the onset of greening up to 72 h. 56 kD protein of major intensity was observed in all greened chloroplasts and 24 kD protein increased remarkablly in both control and spermine-treated cotyledons. The thylakoids from spermine-treated cotyledons showed higher amounts of thylakoid proteins as compared to the controls. The results suggest that spermine may play a role in the regulation of plastid development and stabilizes the membrane function during greening.

Key Words : mung bean cotyledon, chlorophyll-protein complex, plastid membrane protein, spermine, greening

1. Introduction

The naturally occurring polyamines spermine and spermidine and their diamine precursor, putrescine, play important roles in plant growth and differentiation (Evans and Malmberg, 1989). Polyamines have been implicated in the regulation of fundamental processes such as macromolecular biosynthesis, cell division, cell and tissue differentiation, embryogenesis and organogenesis (Smith, 1985 ; Altman, 1989 ; Flores *et al.* 1989). Recently, it has been proposed that polyamines are involved in root growth (Geneve and Kester, 1991; Mirza and Bagni, 1991), flower induction (Wada *et al.* 1994) and initiation of adventitious buds in stem segments (Tanimoto *et al.* 1994).

Polyamine levels increase significantly upon exposure to environmental stress, and it has been hypothesized that they are part of a plant defense mechanism against stress. This hypo-

thesis has been supported by findings in several studies in which exogenously added polyamines have been shown to protect plant tissue from the detrimental effects of several types of stress, including ozone (Bors *et al.* 1989) and chilling (Songstad *et al.* 1990). The protective effects of polyamines in the control of several stress-induced phenomena, are thought to occur through electrostatic binding of polyamines to nucleic acids and membranes (Slocum *et al.* 1984). It has been proposed that polyamines also act as radical scavengers (Drolet *et al.* 1986; Bors *et al.* 1989) or that they stabilize membranes *via* ionic interactions (Tadolini, 1988) to provide protection against environmental stress. When exogenously applied polyamines to aging and detached tissue, polyamines interact with membranes inducing changes which lead to retardation of senescence. In fact, exogenous polyamines are able to preserve chlorophyll retention in thylakoid membranes of barley chloroplasts (Popovic *et al.* 1979) and osmotically stressed oat leaves (Besford *et al.* 1993). However, little information is available on the effect of polyamines on photosynthesis involved in chlorophyll synthesis and formation of plastid membrane proteins during chloroplast development. The present study was undertaken to elucidate the effects of spermine on developmental changes in chlorophyll-protein complexes and plastid membrane proteins of mung bean cotyledons during greening.

2. Materials and Methods

2.1. Growth conditions and treatments

Seeds of mung bean(*Vigna radiata* Wilczek) obtained from a local dealer were sterilized with 1% sodium hypochlorite solution for 15 min, rinsed thoroughly with sterile distilled water and then soaked for 12 h in distilled water in the dark. For the greening experiments, mung bean seeds were grown in vermiculite moistened with distilled water in the dark at 26°C. After germination for 4 days, cotyledons were excised from etiolated seedlings under a dim green safe light and placed in Petri dishes containing filter disks moistened with distilled water or 1.0 mM spermine. The cotyledons were incubated in test solutions for 18 h at 26°C in the dark and subsequently exposed to white fluorescent light with an intensity of 2,000 lux for 24, 48 and 72 h. After illumination, cotyledons were thoroughly rinsed with distilled water, then blotted, weighed and stored at -20°C until analysis.

2.2. Chloroplast isolation

Cotyledons were homogenized with a mortar and pestle in a medium containing 0.5 M sucrose, 50 mM Tricine-NaOH buffer (pH 8.0) and 5 mM EDTA. The homogenate was filtered through 8 layers of cheesecloth and centrifuged at 100 x *g* for 5 min. The supernatant was centrifuged at 4,000 x *g* for 15 min. The chloroplast pellet was washed with 5 mM EDTA (pH 8.0) and centrifuged at 4,000 x *g* for 5 min to obtain chloroplast thylakoids (Tanaka and Tsuji, 1983). All procedures of chloroplast isolation and subsequent preparation of materials used for gel electrophoresis were carried out at 0-4°C.

2.3. SDS-polyacrylamide gel electrophoresis

For the preparation of chlorophyll-protein complexes (CPs), the chloroplast thylakoids

isolated from greened cotyledons were dissolved in 50 mM Tris-HCl (pH 8.8) and 1% SDS and centrifuged at 20,000 x *g* for 15 min to remove insoluble matter. The green supernatant was made up to 0.3 M Tris-HCl (pH 8.8), 10% glycerol and 1% SDS at an SDS/chlorophyll weight ratio of 10 (Tanaka and Tsuji, 1982). CPs were separated by SDS-polyacrylamide gel electrophoresis (PGAE) according to the method of Anderson *et al.* (1978). Electrophoresis was carried out on 8% polyacrylamide separation gel with 4% stacking gel. After electrophoresis, the gel was scanned at 675 nm with a gel-scanner attached to a spectrophotometer (Shimadzu, CS-930).

For the preparation of plastid membrane proteins, membrane samples were dissociated by boiling with 62.5 mM Tris-HCl buffer (pH 6.8) containing 2% SDS, 10% glycerol and 10% mercaptoethanol for 1.5 min, and the membrane proteins were separated by SDS-PAGE. Electrophoresis was performed according to the method of Laemmli (1970). Gels consisted of a 4% stacking gel and 13% separation gel. Electrophoresis was carried out at 20 mA during stacking of the sample proteins, and at 30 mA during separation of proteins. After electrophoresis, the gel was stained with 0.1% Coomassie Brilliant Blue, following by destaining in 12.5% isopropanol-10% acetic acid and storing in 7% acetic acid. Stained gels were scanned at 570 nm. Bovine serum albumin (68,000 dalton), ovalbumin (43,000 dalton), carbonic anhydrase (29,000 dalton), lysozyme (14,300 dalton) and ribonuclease (13,700 dalton) were used as molecular weight standards. Molecular weight estimation was based on the method of Weber and Osborn (1969).

3. Results

3.1. Effect of spermine on chlorophyll-protein complexes(CPs) Pattern

Cotyledons excised from mung bean seedlings

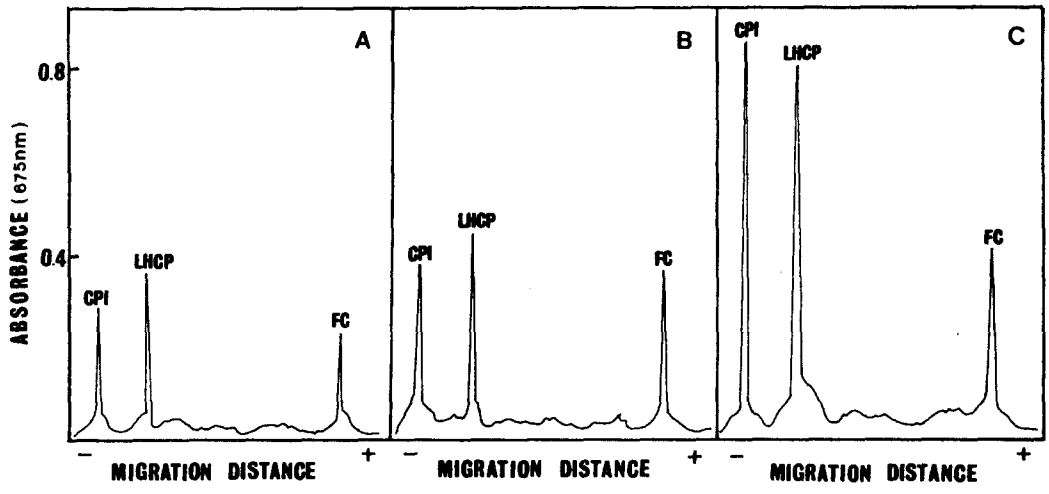

Fig. 1. Densitometer tracings of chlorophyll-protein complexes isolated by SDS-polyacrylamide gel electrophoresis of chloroplast thylakoids from control cotyledons illuminated for 24 h(A), 48 h(B) and 72 h(C). CPI, P 700 chlorophyll a-protein complex; LHCP, light-harvesting chlorophyll a/b protein complex; FC, free chlorophyll.

were incubated in 1.0 mM spermine solution for 18 h in the dark and subsequently exposed to white fluorescent light for up to 72 h. Analysis by SDS-PAGE of the chlorophyll-protein complexes (CPs) composition of the thylakoids extracted from cotyledons is shown in Fig. 1. PAGE of SDS-digested chloroplasts revealed two main chlorophyll proteins, the light-harvesting chlorophyll a/b protein (LHCP) and the chlorophyll-protein of the pigment system I (CPI), which exhibit different chlorophyll and carotenoid composition. During the lag period that preceded the accumulation of chlorophyll, a small amount of CPs appeared and the amount of CPs increased with accumulation of chlorophyll during greening. The results are consistent with the observations of others (Markwell *et al.* 1979 ; Shimada et al. 1990 ; Nock *et al.* 1992). LHCP was the predominant CP in early phase of greening. After 72 h illumination, a large amount of CPI and LHCP were formed and CPI peak exceeded the LHCP one.

When seedlings were treated with spermine, a large amount of CPs accumulated rapidly than they did in untreated controls during 48 h of illumination (Fig. 2). The patterns of increase in levels of CPs during greening were quite similar in both control and spermine-treated samples, though the amount of CPs of the spermine-treated samples decreased slightly in the late phase of 72 greening.

3.2 Effect of spermine on plastid membrane proteins

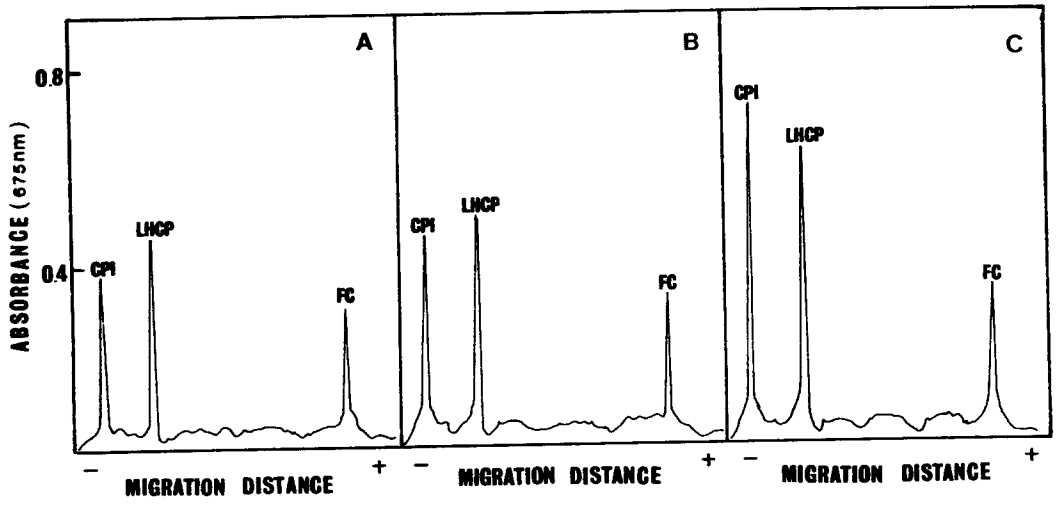

Fig. 2. Densitometer tracings of chlorophyll-protein complexes isolated by SDS-polyacrylamide gel electrophoresis of chloroplast thylakoids from spermine-treated cotyledons illuminated for 24 h(A), 48 h(B) and 72 h(C). CPI, P 700 chlorophyll a-protein complex; LHCP, light-harvesting chlorophyll a/b protein complex; FC, free chlorophyll.

To obtain the profiles of plastid membrane proteins during greening, polypeptides of thylakoid membranes were analyzed by SDS-PAGE. Etioplasts and thylakoids of chloroplasts were comprised of different components of proteins

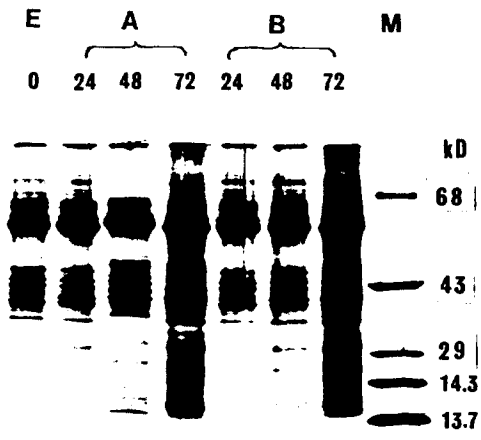

Fig. 3. Develpomental changes in protein composition of the plastid membrane during greening. From left to right, successive slots contain proteins from plastids isolated after 0, 24, 48 and 72 h illumination. E, etioplast; A, control cotyledons ; B, spermine-treated cotyledons ; M, markers.

(Fig. 3). Proteins of plastid membrane were separated into about 30 bands. The protein species changed quantitatively and qualitatively in cotyledons with progress of exposure to light. Protein bands with high molecular weight protein were observed concomitantly in etioplasts and chloroplasts. As greening proceeded, low molecular weight protein bands appeared as abundant species (Fig. 4). The proteins of the plastid membrane could be divided into three groups on the basis of the time of their appearance during greening. The first group included the proteins which are present in etioplasts and mature chloroplasts, and do not appear to change during greening. The molecular weight of the most prominent of these proteins was 56 kD. The second group was comprised of proteins which were small or absent from etioplast and appeared during greening. The molecular weight of these proteins was 24 kD, a major thylakoid polypeptide in these samples. The third group included the proteins which were present in large quantities in etioplasts and chloroplasts. These had molecular weight of 36 kD. Fig. 5 shows the profiles of plastid membrane proteins from spermine-treated cotyledons after greening. Two protein bands

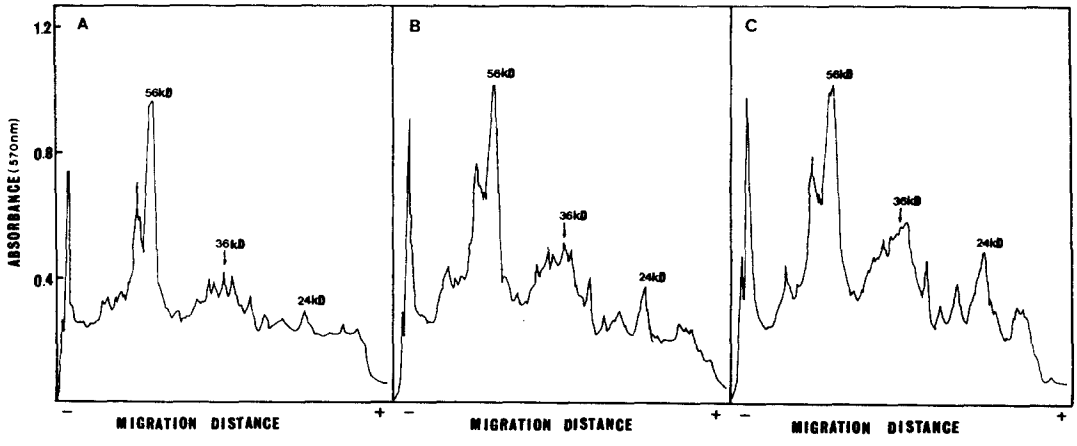

Fig. 4. Electrophoretic profiles of plastid membrane proteins from control cotyledons illuminated for 24 h(A), 48 h(B) and 72 h(C).

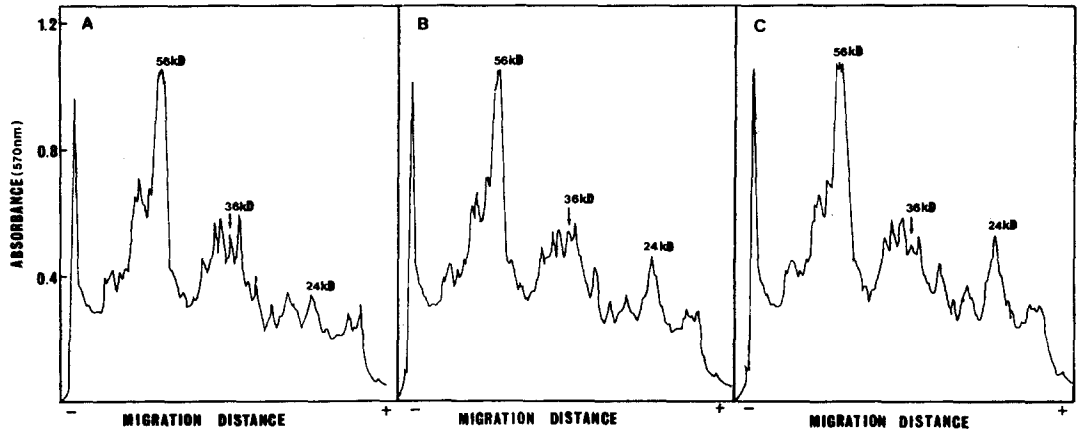

Fig. 5. Electrophoretic profiles of plastid membrane proteins from spermine-treated cotyledons illuminated for 24 h(A), 48 h(B) and 72 h(C).

(56 kD and 24 kD) were also distinctly detected in spermine-treated plastids during greening. High molecular weight bands (56 kD) of major intensity were observed in plastid and were maintained dorminant in all samples. A low molecular weight band (24 kD) was also increased in spermine-treated chloroplasts. The electrophoretic patterns of chloroplast membrane polypeptides from cotyledons treated with water and spermine were indistinguishable from each other. However, in the spermine-treated preparations, thylakoid membranes contained higher amount of thylakoid proteins as compared to the untreated samples, with increase of background throughout the track (Fig. 5 C).

4. Discussion

Development of etioplasts to chloroplasts is triggered by light. Upon illumination, protochlorophyllide is phototransformed and a rapid transformation of etioplasts into chloroplasts occurs with the visible result of greening of the plant due to the synthesis of chlorophylls. Parallel to chlorophyll accumulation, a rapid formation of thylakoid membrane occurs, leading to the assembly of a photosynthetically competent chloroplast. Light-induced chloroplast development accompany active synthesis of chlorophyll-proteins. Although chlorophyll and CPs were absent from dark-grown mung bean cotyledons, they began to accumulate with illumination (Fig. 1). Shimada *et al.* (1990) reported that the rates of formation of different CPs were regulated by the relative rates of synthesis of chlorophyll a and apoproteins and by differential affinities of the apoproteins for chlorophyll a. Thus, CPs may play an important role in the functional and structural development of photosynthetic apparatus. The stabilizing interactions of pigment and protein turnover represent a way of ensuring stoichiometry between components of complexes at the post-transcriptional, point-of-assembly level (Nock *et al.* 1992). The newly synthesized CPs assemble to form photosystems. During the light-induced greening a massive incorporation of the

chlorophyll-binding proteins into thylakoid membranes occurs. Thylakoid membranes of higher plants contain several chlorophyll-proteins which play important roles in the light harvesting and photochemistry of photosynthesis. In the photosynthetic membranes, LHCP apoprotein is subjected to turnover after transfer of plants from light to darkness (Bennet 1981). This suggests that LHCP in the early phase of greening differs in stability from that of mature chloroplasts. LHCP was the main CP of thylakoid membrane of mung bean cotyledon in the early phase of greening and the amounts of other CPs were very small. As greening proceeded, the percentage of total chlorophyll associated with CPI increased in accordance with a increase in the ratio of LHCP. Protein subunits of LHC have been reported to show such characteristic increases during greening (Tanaka and Tsuji, 1982). Bennet *et al.* (1987) reported that neither LHC of PS II nor LHC of PS I was detected when the rate of synthesis of chlorophyll was low under weak illumination. Intermittent exposure to light, with long intervals of darkness, inhibited the accumulation of chlorophyll b and LHC of PS II (Tzinas *et al.* 1987). In this study, one point was clarified by gel electrophoresis. In the early phase of greening LHCP most actively accumulated in both control and spermine-treated plants, whereas other CPs were at low levels, suggesting that some unstable CPs exist in the early phase of greening (Figs. 1 and 2). With progress of greening, the relative amount of CPI to total CPs increased, and probably resulting in stabilization of all the chlorophyll. Thus, chlorophylls could not be easily released from its apoproteins. Unstable CPs in the early phase of greening must be an intermediary stage in the course of ultimate, stable CPs. We found previously that treatment of mung bean plants with polyamines prevent the loss of chlorophyll, indicating preservation of the thylakoid membranes at the site of the CPs (Hong, 1993). Application of spermine or spermidine were effective in retarding the loss of proteins from the thylakoid membranes of osmotically stressed oat leaves (Besford *et al.* 1993).

Stability of thylakoid polypeptides requires a well-developed and integral thylakoid membranes. In the profiles of plastid membrane proteins of mung bean cotyledons during greening, quantitative and qualitative changes were observed in both control and spermine-treated samples (Figs. 4 and 5). During greening, three classes of plastid membrane proteins could be distinguished in mung bean cotyledons. The 36 kD proteins seemed to be present in etioplasts and disappeared during greening, and the 24 kD proteins seemed to be absent in etioplasts and appeared during greening. Finally, 56 kD and 59 kD proteins and several others were present in both etioplasts and chloroplasts. As greening proceeded, increase of the 24 kD protein was particularly remarkable. The 24 kD protein is considered to be a subunit of light harvesting chlorophyll. The 56 kD and 59 kD proteins are considered to be subunits of chloroplast coupling factor 1 (CF 1), respectively, because their mobility is identical to that of spinach CF 1 subunits (Ohya *et al.* 1980).

Treatment of spermine increased the LHC level of thylakoid polypeptides at the site of CPs during illumination. The results indicates that high level of polyamine and its metabolites play a protective role in maintaining the composition of these membranes. The similarity in appearance of CP bands during greening of spermine-treated cotyledons provides further evidence for the stabilization of these membranes by spermine. Many of the biological

functions of polyamines are attributable to their cationic nature. They are highly protonated at physiological pHs which should favor electrostatic binding of polyamines to nucleic acid and negatively charged functional groups of membranes and proteins (Slocum *et al.* 1984). Thus, polyamines can bind to the negatively charged phospholipid head groups on membranes, thereby influencing stability and permeability characteristics of these membranes. Roberts *et al.* (1986) have shown that amines, especially spermine and spermidine, at a physiological concentration rigidify membrane surfaces. This observation indicates that polyamines may play a role in determining membrane fluidity. The electrophoritical evidence from this study suggests that polyamines stabilize the composition of thylakoid membranes during greening adding further support the view that polyamines are directly involved in preventing degradation of CPs during osmotic stress and polyamines play a role in preserving the integrity of these membranes (Besford *et al.* 1993). The mechanism probably involves both direct binding of polyamines to the membranes, thereby preventing lipid peroxidation and proteolytic attack, and inhibition of ethylene synthesis through inhibition of ACC synthase (Fuhrer *et al.* 1982 ; Drolet *et al.* 1986 ; Winer and Apelbaum 1986) by restricting accumulation of ACC-synthase transcripts (Li *et al.* 1992).

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녹화중인 녹두 자엽의 엽록소-단백질 복합체 및 색소체막 단백질의 변화에 미치는 Spermine의 효과

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Spermine이 녹화중인 녹두자엽의 엽록소-단백질 복합체(CPs) 및 틸라코이드막 단백질의 변화에 미치는 효과를 조사하였다. 녹화가 진행됨에 따라 CPs형성이 촉진되었으며, 특히 광계 I의 엽록소-단백질(CP I)이 다량 축적되었다. 광수확 엽록소 단백질(LHCP)은 48시간의 초기 녹화과정에서 중요한 단백질로 나타났다. Spermine처리는 초기녹화과정에서 틸라코이드막의 CPs 축적에 효과적이었다. 색소체막 단백질은 녹화과정에서 많은 변화를 나타내었는데, 56 kD 단백질은 전 엽록체에서 다량 관찰되었고 24 kD 단백질은 전 처리구에서 뚜렷한 증가를 보여주었다. Spermine처리에 의해 틸라코이드막 단백질 형성은 대조구에 비해 다소 증가되었다. 이러한 결과들로부터 spermine은 녹화과정에서 색소체의 발달과 색소체막의 안정화에 중요한 작용을 하는 것으로 생각된다.