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THE EFFECT OF SHORT LIGHT-DARK CYCLES ON THE MEMBRANE SYSTEM OF BEAN CHLOROPLASTS

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Abstract

The effect of alternating 30–15, and 15–7.5 min. light-dark cycles (LDC) as well as of 16 hours long-day illumination and 8 hours dark were studied on 4 week old Valja bean grown in phytotron. In every case the daily period of illumination was 16 hours, the light flux density was 32 Wm^{-2}, the temperature was 21 ± 1 °C.

The short rhythms were unfavourable for the development of beans. Compared to the 16–8 hours LD control the accumulation of dry-matter decreased, necrotic patches appeared on the yellowishgreen leaves. The characteristic effect of the short LDC-s on the structure of the chloroplasts was that the starch was almost completely missing from the plasts, the thylakoid number per grana decreased, the stroma lamellae and end granal membrane lengths per unit surface considerably increased. The ratio of the grana composed of 2–5 thylakoids manifested four-five times increase in the 30–15 and 15–7.5 min. LDC-s compared to the 16–8 hours control. The granal intrathylakoidal spaces expanded. In one part of the plasts the membranes of the columnar grana became swollen and disorganized.

Key-words: light-dark cycles, chloroplast, grana, stacked membranes, unstacked membranes, dry matter, bean.

Introduction

The length and proportion of light-dark periods (LDP) significantly change the pigment-content, membrane structure of chloroplasts, the pH relations of the intrathylakoidal space and stroma plasma (MARÓTI, 1982; MARÓTI and PATAKY, 1982). The 30–15, 15–7.5 min. alternating short LDP-s imply strong "light-dark stress" on the development of several plants. They become yellowish-green, the chlorophylls and carotenoids show significant and specific disorganization, necrotic patches appear on the leaves.

Depending on genotype, the dry-matter production either increases or decreases.

The length of the dark period and the ratio of light-dark, resp., have great effect on the membrane organization of chloroplasts (ARMOND et al., 1976; DAVIS et al., 1976; AKOYUNOGLOU and ARGYROUDI—AKOYUNOGLOU, 1978).

In greening experiments where the light-dark ratio varies between 1/10–1/90 — ie. the rather short (0.01 sec. — 2 min.) and short (2–15 min.), resp. light periods are followed by long dark periods — characteristic changes are observable: no normal grana are formed, only so-called double primary thylakoids. The ratio of chlorophyll a/b is high. The oxygen evolution is hindered (STRASSER and BUTLER, 1976). The cation regulation of the chlorolpasts is decreased. Less chlorophyll-protein complexes

are formed than in continuous illumination (ARGYROUDI—AKOYUNOGLOV et al., 1971; SÁRVÁRI and GEIGLER, 1982).

The effects of the short (30–15 and 15–7.5 min.) 2/1 proportioned light-dark periods applied by us essentially differ from the above; normal grana develop, the ratio of chlorophyll a/b is only slightly higher than in the 16–8 hours control LDP, the plants flower and produce. The changes in the membrane system of the chloroplasts are generally not so drastic as in the case of short light-long dark treatments. Therefore, our electronmicroscopic studies serve with data to the relationship between the membrane structure and utilization of light.

The present paper reports on the changes of chloroplasts of the 3rd leaf of 4 week old beans grown in 30–15 and 15–7.5 min. LDP-s, compared to the 16–8 hours control. Attempt was made firstly to correlate the degree of thylakoid aggregation, the amount and ratio of stacked and unstacked membranes with dry-matter production.

Material and Methods

The studies were performed on *Phaseolus vulgaris* L. c. v. Valja beans. The plants were grown in phytotron (HORVÁTH, 1972), in the mixture of sand-perlite 1:1, with nutrient of HOAGLAND (REYSS and BOURDU, 1970). The moisture content of the soil was 70% of the water capacity. The nutrient suplly was ensured by 20 ml nutrient solution twice a week, the original humidity of the soil was maintained by daily watering with distilled water. The daily amount of light was the same. The control plants were grown in 16 hours continuous illumination and 8 hours dark. In the short-rhythm experiments alternating periods of 30 min. light, 15 min. dark, and 15 min. light, 7.5 min dark were applied. The light flux density was 32 Wm^{-2} in the climate chambers, using F_{29} light tubes. Table 1 comprises the spectral energy dispersion of the light tubes. The plants were grown at constant temperature of 20±1 °C.

For electronmicroscopic studies the samples were taken from the central part of the lateral leaflet of the 1. tripartite leaf at the age of 4 weeks. The leaf pieces with diameters of 0.5–1 mm were fixed in 3% glutaraldehyde, contrasted with 2% $KMnO_4$ solution, dehydrated in ethylalcohol series, and embedded into Durcupan ACM resin. The sections prepared with Reichert ultramicrotome were stained with Pb citrate.

The pictures of the chloroplasts of the mesophyll palisade parenchyma were prepared by Tesla BS 212 E and Tesla BS 500 electronmicroscope. The planar size of the plasts, the number and size of the grana, the grana/thylakoid number as well as the length and ratio of stacked and unstacked membranes were measured on pictures of known magnification. 30–40 plasts were evaluated per treatment.

Table 1. Energy dispersion of F29 light tubes in the % of energy falling to the 400-700 nm wave domain.

Violet 400–436 nm	Blue 436–495 nm	Green 495–560 nm	Yellow 560–589 nm	Orange 589–627 nm	Red 627–700 nm
2.25	7.38	18.06	22.87	29.21	20.23

Results

In the experiments both the 30–15 min. and 15–7.5 min. light-dark periods decreased the production of the plants. As the results of the short periodical illumination the total dry-matter production decreased to about the half. In tendency the organic dry-weight followed the trend of the total weight.

The dry-matter accumulation was the lowest in the 30–15 min. LDP, being only 40% of that of the control plants. This is firstly the consequence of the more considerable reduction in stem and leaf weights (Table 2).

Table 2. Dry-matter production (related to 1 plant). The data are the average values of 25–25 plants per treatment. Processing was accomplished at four weeks of age.

Light treatment	Dry weight mg/plant						
	root	stem	primordial leaves	1. tripartite leaves	2. tripartite leaves	3. tripartite leaves	total
16–8 hours LDP	332	273	63	129	116	98	1012
30–15 min. LDC	133	141	39	48	49	56	466
15–7.5 min. LDC	137	179	33	62	55	74	540

The size of the chloroplasts of the palisade parenchyma was enhanced by the short light-dark cycles (Table 3). The shape of the chloroplasts changed; they became elongated and flattened.

A large amount of starch was found in the chloroplast of plants exposed to long-day (16–8 hours) LDP. 35% of the section-surface of the chloroplasts contained starch, the membrane system was found to aggregate at the peripheral areas (Plate I, Table 1 and 3).

Table 3. The effect of short periodical treatment on the structure of chloroplasts. The plasts of the palisade parenchyma of the 1. tripartite leaves were evaluated. The data are the average values of 30–40 chloroplasts.

Light treatment	Chloroplast section area (μ^2)	Proportion of area %		Number of grana (10 μ^2)	Stroma lamellae (μ/μ^2)	Partition leghth (μ/μ^2)	End granal membrane (μ/μ^2)	Proportion of stroma lamellae to total lamellar material (%)	Proportion of partition to total lamellar material (%)	Proportion of end granal membrane to total lamellar material %
		starch	grana							
16–8 hrs LDP	11	30	22	25	1.86	3.19	1.16	30	52	18
30–15 min. LDC	19	2	13	11	3.41	3.32	1.78	40	39	21
15–7.5 min. LDC	18	2	13	21	2.78	4.09	2.64	30	43	27

The assimilatory starch did not accumulate in the chloroplasts of bean leaves grown in short periodical illumination. The amount and surface ratio of the grana (Table 3).

The number of grana per section-surface increased on the effect of 15–7.5 min. LDP-s and decreased on that of 30–15 min. periodical illumination. Converted into unit surface the degree of decrease in the amount of grana (more than 50%) was rather significant in the 30–15 min. light-dark periods.

In the leaves grown under continuous 16 hours illumination the surface ratio of the grana amounted to about 22% of the cut-surface of chloroplasts. The area of grana was reduced to nearly the half by the short cycles, from the whole sectionsurface the quota of grana was 13% in the case of both LDC-s. The effect of short periodical illumination on the shape of grana and the amount of grana/thylakoid (Fig. 1).

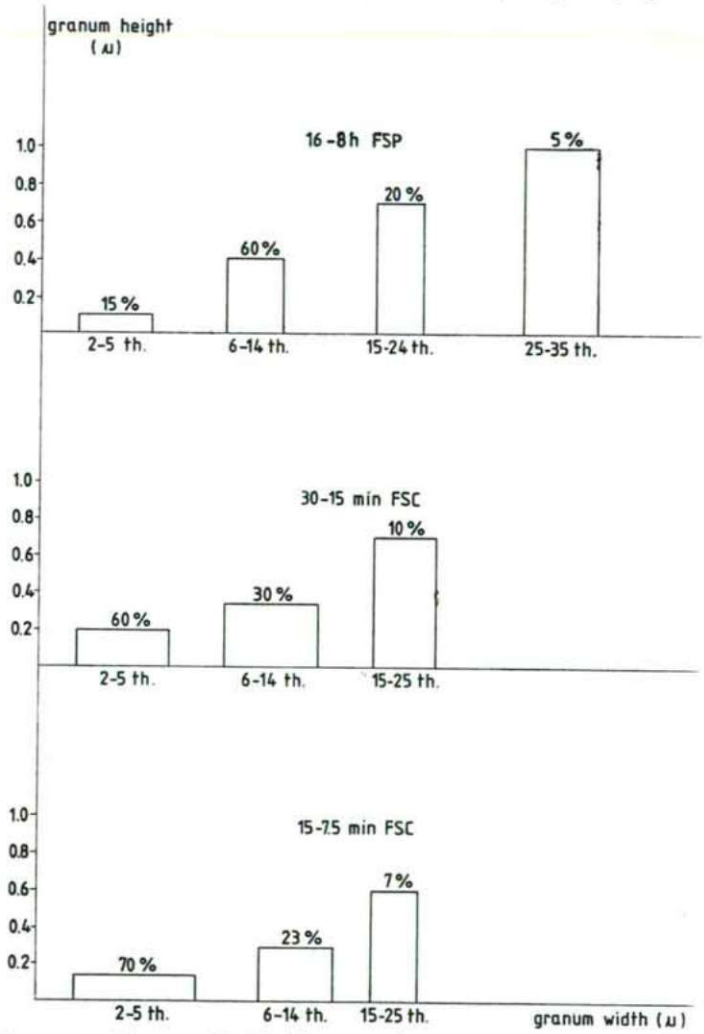

Fig. 1. Size of grana and degree of thylakoid aggregation.

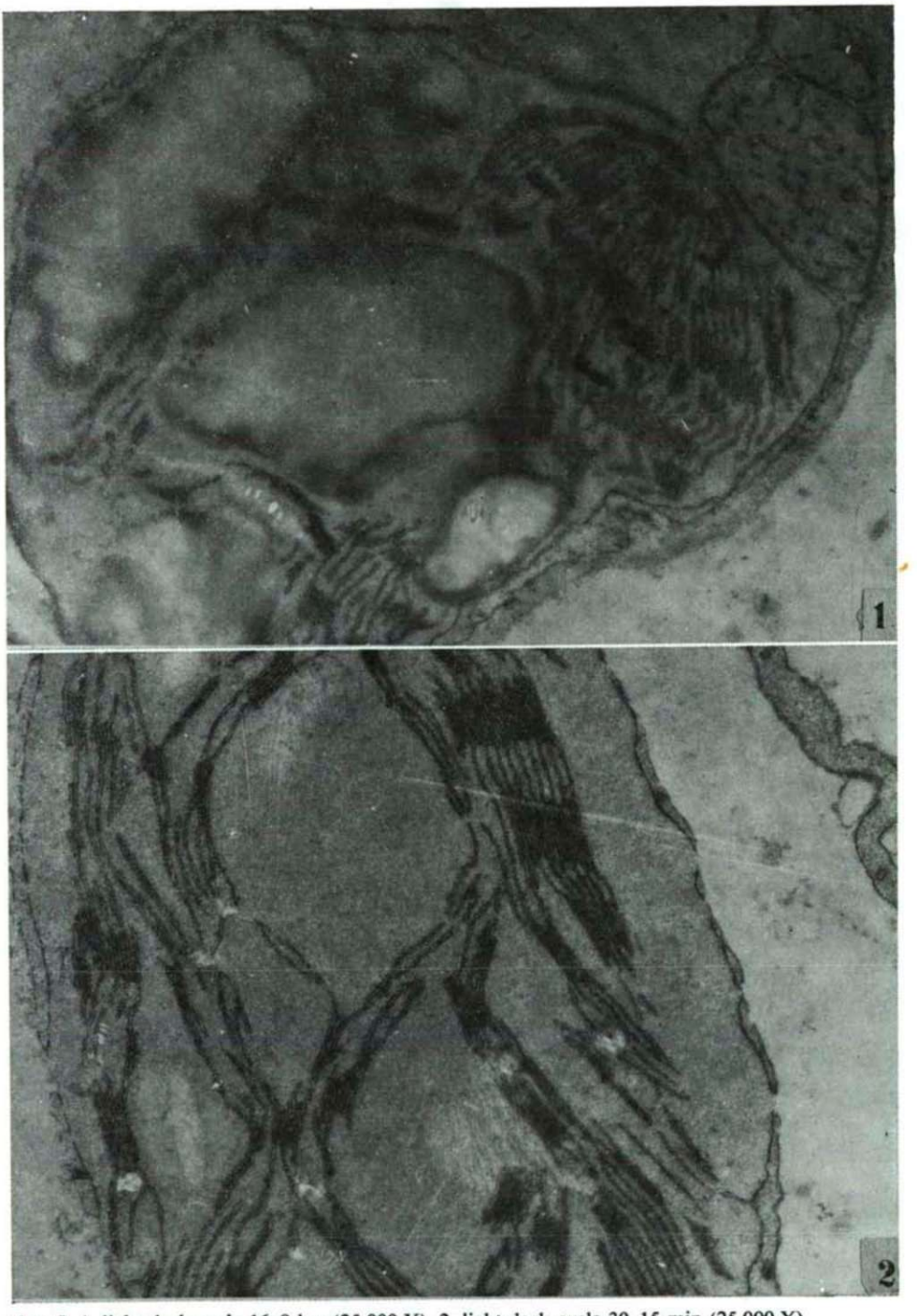

Plate I. 1. light-dark cycle 16–8 hrs (25 000 X), 2. light-dark cycle 30–15 min (25 000 X).

a. The size, height and width of the grana

On the basis of the thylakoid aggregation the grana were separated into 4 groups: standing of 2–5; 6–14; 15–24, and 25–35 thylakoids.

The percental distribution of these four groups was also evaluated.

In the chloroplasts of leaves growing in continuous light the grana made up of 6–14 thylakoids were dominating, giving 60% of the total amount of grana.

Due to the multiple adherence of the thylakoids the frequency of the grana composed of 15–35 compartments was 25% in the control chloroplasts. The grana having 2–5 thylakoids occurred in lowest number, their shape differed from the rest, the diameter of their width surpassed their height measures.

Regularity, tight correlation was observed between the degree of thylakoid aggregation and the grana shape. The partition of the multithylakoidal grana was short, the height/width ratio was high. With the decrease of thylakoid aggregation the adhering surface of certain grana compartments became larger.

On the effect of the periodical treatment, there was a change in the membrane organization of the chloroplasts.

The uniform effect of the short rhythms was that the 25–35 thylakoidal, columnar macrograna did not develop and the ones standing of 2–5 thylakoids occurred in 50–70%.

Chloroplasts of varying membrane structure developed on the effect of 30–15 min. light-dark cycles. The heterogeneous plasts could be divided into three groups. Only one kind of chloroplast could be found within each palisade cell.

1. The chloroplasts having granum structure, similar to those of the long-day illumination occurred in the highest amount, forming 55–60% of the studied plasts (Plate I/2). Less high and wider grana developed in these chloroplasts. The 2–5 thylakoidal grana were the most frequent; 60% of the total amount of grana.

The grana joined by 5–14 compartments were also frequent (30%), and the ones containing 15–25 thylakoids occurred in about 10%.

The average thylakoid number of the grana decreased to almost the half compared to the control. The smaller degree of aggregation was compensated by higher partition. The shape of the grana made up of similar amount of thylakoids changed in the 30–15 min. LDC, the partitions became longer (Fig. 1).

2. In one part of the chloroplasts (25%) the grana intrathylakoidal spaces widened. The loculi found at the end granal membranes dilated into ducts having wide cavities and at many places into wide sacks. The cavity of the thylakoid loculi also varied within the grana. Many vesicules could be found at the end of the stroma lamellae, furthermore the interlamellar spaces also strongly widened (Plate II/1). The degree of aggregation of the thylakoids and the value of the grana surface ratio were similar to that of the previous group.

Thus, destructive processes appeared in the chloroplasts on the effect of the 30–15 min. LDC-s, becoming the general characteristics of the chloroplasts. On the effect of treatment the terminal vesicules of the grana, being contiguous with the stroma became swollen, the detached wall of the vesicules showed undulatory contour.

The swelling not only appeared in the case of the vesicules having terminal location, but also in the stroma thylakoids, the diameter of the isolated, long lamellae was also dilated (Plate II/3). These processes of swelling were not characteristic to every chloroplast membrane, however, these manifestations commenced in 25%

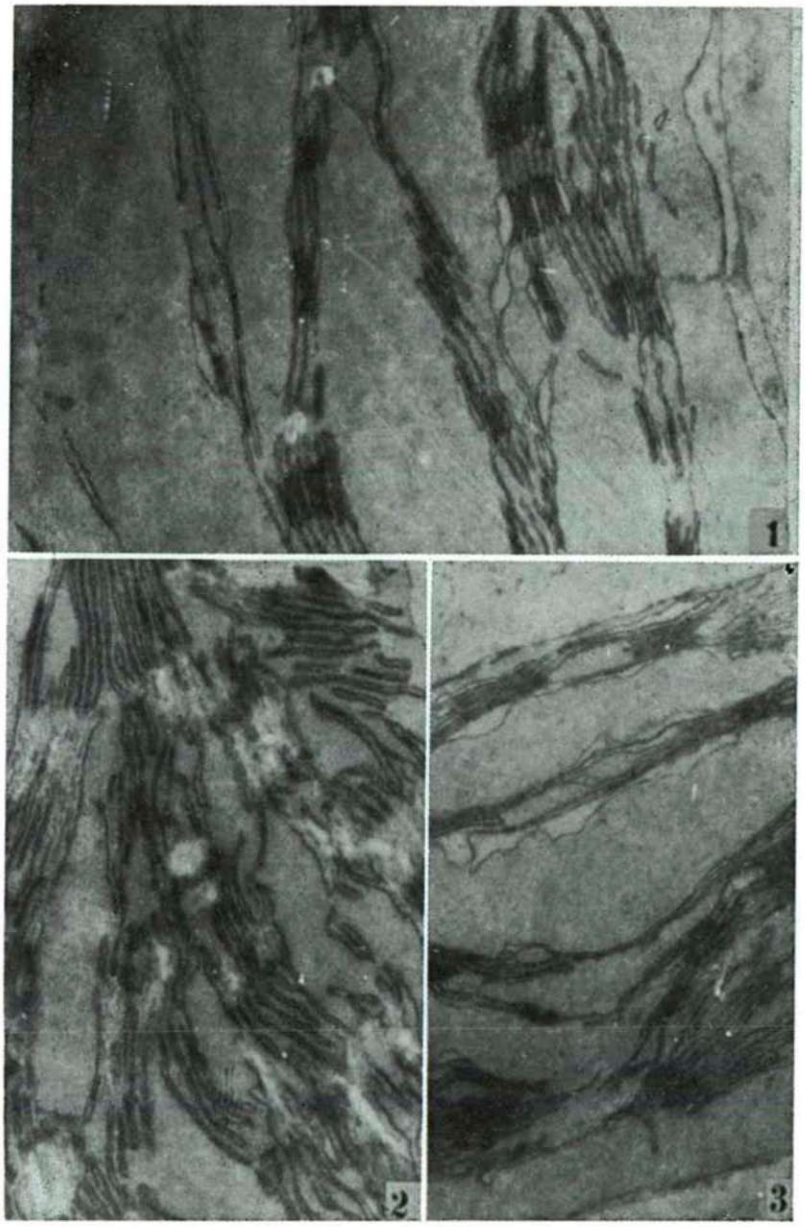

Plate II. 1. light-dark cycle 30–15 min (25 000 X), 2. light-dark cycle 30–15 min (25 000 X), 3. light-dark cycle 30–15 min (25 000 X).

of the studied chloroplasts, to a lesser or higher degree. The sporadical, short stroma lamellae took up undefined shape and undulatory contour.

3. In close to 20% of the studied chloroplasts the columnar grana became completely swollen, the membranes became resolved. In the chloroplasts contrasted with $KMnO_4$ the spaces of the grana appeared as white patches, the chloroplasts showed mosaic appearance. In these chloroplasts the stroma lamellae dominated. It is presumably the destructive effect of the dark periods of the short cycles which manifested, even affecting destructively the intact, developed chloroplasts (Plate II/2).

The 15–7.5 min. LDC-s considerably decreased the average thylakoid number of the grana compared to the 16–8 hours long-day illumination. The significant reduction in thylakoid aggregation was shown by the 70% occurrence of the 2–5 thylakoidal grana. Compared with the control the grana were wider, the adhering surface of each grana disc became larger. The grana made up of 15–22 thylakoids occurred in 7% (Plate III/1).

The granal intrathylakoidal spaces became dilated, the expansion of the loculi was firstly detectable in the case of the therminal grana thylakoids. Decomposition could not be observed in the membranes of the grana (Plate III/2).

b. Ratio of Stacked and unstacked membranes

The light-dark cycles substantially changed the membrane organization of the chloroplasts.

The stacked membranes (partition) and the unstacked membranes (stroma lamellae+end membranes) were evaluated in respect to their lengths falling to unit surface and their proportion regarding the total membrane lengths.

In the 16–8 hours treatment the ratio of stacked. membranes was strikingly high, the thylakoid membranes were made up of partitions in more than 50%. The proportion of the end granal membranes was 18% to the total membrane lengths, and that of the stroma lamellae was 30%. Even concerning unit area the length of the partition membranes was the greatest.

In 30–15 min. light-dark periods the ratio of the stacked and stroma lamellae was identical (40%). The distribution of the grana standing of few (2–5) and many (7–22) thylakoids was found to be close to similar.

The ratio of the unstacked membranes (stroma+ end membrane) was 60%, being higher than that of the partitions (40%). Compared to the control a significant increase was experienced in regard to the ratio of the stroma lamellae, this being of slighter degree in the case of the end granal membranes.

The end granal membrane lengths regarding surface unit increased from 1,1 μ to 1,8 μ, since the grana became wider with the lower degree of aggregation. At the same time the percental quota of the stacked membranes decreased from the total membrane length.

The value of the total membrane length falling to 1 μ^2 was higher in the case of the 30–15 min. LDC than in the control plasts; in the latter the value of lamellation per unit area was 6 μ, which increased to 8,5 μ in the 30–15 min. LDC.

Compared to the 16–8 hours long-day illumination the 15–7.5 min. light-dark cycle significantly increased the ratio of end granal membranes on the one part (by 10%), on the other part it decreased the percental quota of the partition — also by 10%.

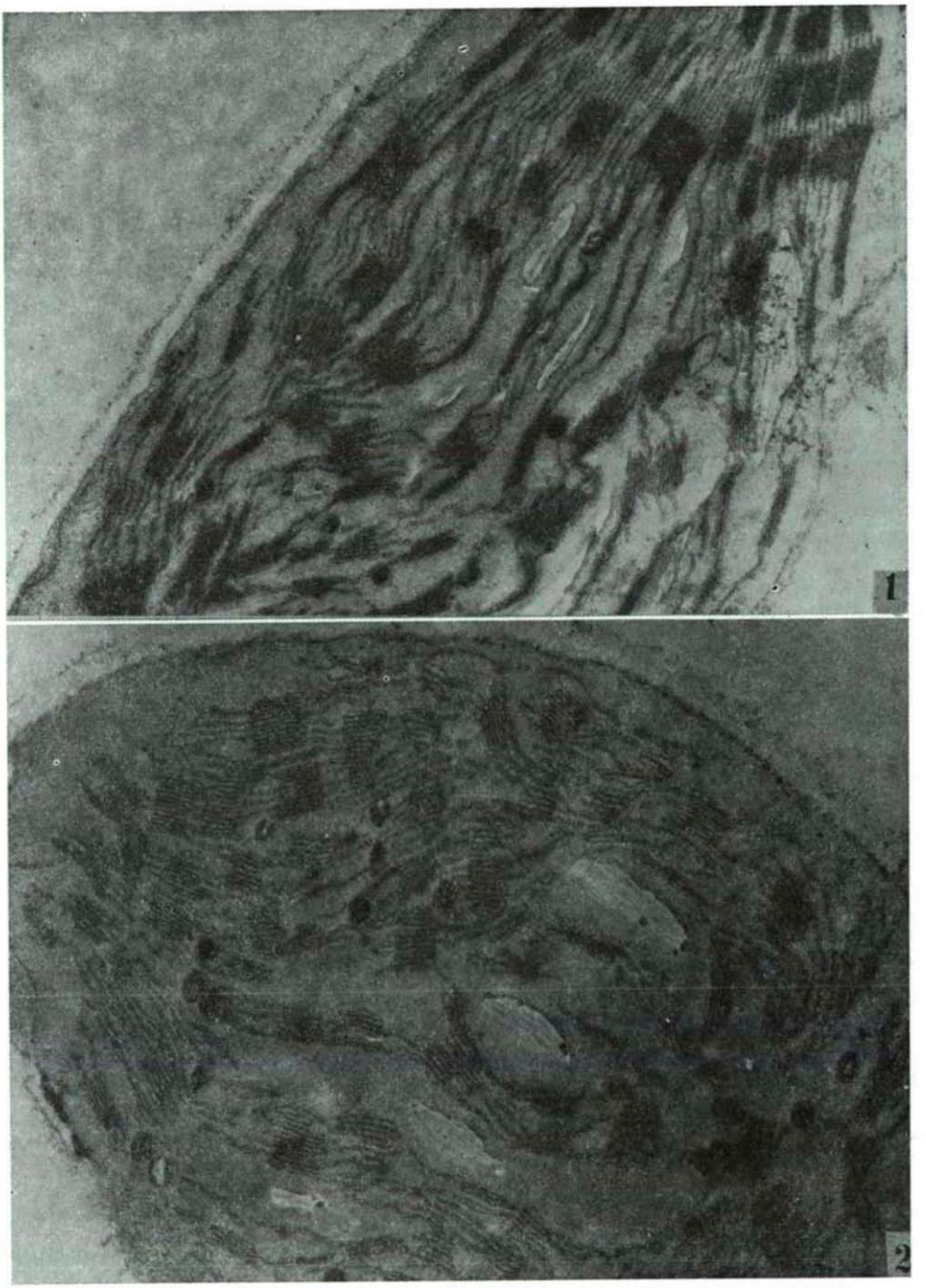

Plate III. 1. light-dark cycle 15–7.5 min (25 000 X) 2. light-dark cycle 15–7.5 min (25 000 X).

The partition length regarding unit area of the plasts surpassed the value of the other two light-treatments. The length of the total membrane system observed at an area of 1 μ^2 showed maximal values in the case of the 15–7.5 min. LDC. It was the surface of the end granal membranes which increased in the highest degree, surpassing twice the values of the control plants. This alteration could be explained by the increase in the amount of grana.

Discussion

The effect of light-treatments different from the natural rhythm — in the case of identical light intensity and illumination periods — is determined by the length of the light-dark periods.

The control plants as well as those treated with light-dark periods received light of the same intensity. The daily total energy amount was also identical. Despite this, the alternating light-dark cycles resulted changes differing from the control. The rhytmic illumination caused a change in the photosynthetic structure.

The utilization of light depends fundamentally on the organization of the chloroplast's membrane system, the size of the membranes, the degree of thylakoid aggregation, and the ratio of unstacked and stacked membranes.

The light-dark cycles varying between 1 to 30 munites have in general unfavourable effect on the development of the plants. In these cycles the leaves become yellowish-green, and the appearance of necrotic patches can be detected. There is a decrease in the accumulation of dry-matter, the chlorophylls and carotenoids become significantly decomposed, and in the latter stage of ontogenetic development the leaves become white as the consequence of destruction regarding the photosynthetic apparatus.

The 30–15 min. LDC-s have decreasing or increasing effect on the dry-weight of the plants — depending on the type. The fact can be evidenced best in the case of this cycle that in the light-dark periods of lengths from 5 min. to 6 hours the photosynthetic utilization of light varies according to types (FÜLÖP, 1982; MARÓTI and MIHALIK, 1982; MARÓTI and PATAKY, 1982).

In the case of the Valja bean both short cycles decrease the total production of the plants. The leaf production decreases to smaller extent in the 15–7.5 min. LDC; the dry-weight of the leaves is higher in this cycle than in the 30–15 min. LDC.

It is our assumption that the degradation of the dry-matter is not caused by the accumulation in primary products, but by the destruction of the chloroplasts.

The effect of the light-treatments on the structural state of the plasts is also well shown by the main product of the chloroplasts, the starch. The starch found in high amount and huge proportions in the plasts of the control leaves refers to the intensive course of photosynthesis. Active starch synthesis can be manifested, the formed enormous starch grains fill out 30% of the chloroplast volume. In the leaves grown under short cycles only low amount of starch occurs in the chloroplasts (1–2%).

The question arises, what relationship exists between the changes in the shape, amount and area ratio of the grana and the distribution of the adhered and single membranes?

The number of grana was altered differently by the two kinds of short cycles. A decrease was observable in the 30–15 min. LDC, while in the 15–7.5 LDC the

granum number per cut surface was 30% more than in continuous light, and the area ratio decreased to almost the half. The area ratio of the grana depends on the number of grana and grana vesicules. In the 30–15 min. light-dark cycle the area ratio of the grana decreased proportionally with their amount.

In one part of the chloroplasts of the plants grown under this cycle the structural destruction was irreversible, the grana thylakoids became completely decompodes, whole grana "disappeared"; here the depression of the photosynthetic CO_2 assimilation is presumably of higher degree which could also be evidence in the smallest leaf product.

The highest amount of grana developed in the 15–7.5 min. LDC, the large grana became disjointed, the quota of the smaller grana increased. The fact that the number of grana increased by 30% compered to the control, and their quota from the cut surface decreased almost to the half is partly the result of the change also in the size and shape of the chloroplasts. The length per width ratio of the chloroplasts increased since they became elongated and flattened. The smaller part of the larger plasts was occupied by the grana. On the other hand, there was also a decrease in the size of the grana. Firstly the increase of the stroma plasma was observable. The degree of chloroplast-organization was followed with attention by the values and distribution of the grana and stroma lamellae, as well as the stacked and unstacked membranes, resp.

The flattening of the chloroplasts is also in connection with the thylakoid number per granum. The ratio of stacked and unstacked membranes shifted to the benefit of the unstacked membranes (stroma + end granal membrane) in the case of the short cycle plasts. This is significant in the 15–7.5 min. LDC, where there are more grana and the end granal membranes are longer.

The end granal membrane length falling to 1 μ^2 and the quota of the end membranes from the complete membrane system are the greatest; as well as the length of partition per unit area.

The lamellar system is the most developed in the 15–7.5 min. LDC from the three light-treatments, and this is where the total thylakoid length per 1 μ^2 is the largest.

Studying the relationship between the light utilization and the membrane system of the chloroplasts (BJÖRKMAN, 1975; BOARDMAN et al., 1974; LICHTENTHALER, 1981; PRENZEL et al., 1980) it becomes evident from the works of the listed authors that the formation of grana is greatly influenced by the intensity of illumination. Low light intensity or reduced radiance is favourable for the development of grana, and the surface of membranes per unit area is rather large.

The structure of the chloroplasts developing on the effect of the short cycles applied in our experiments is similar to the shade type chloroplasts, in so far as no starch is accumulated, the grana are wider, less grana can be found per unit surface, and the total thylakoid length per unit area is rather high.

There are sifferences, however, in regard to the degree of thylakoid aggreation, as the adnating percentage of the thylakoids is lower.

In the rhytmic chloroplasts the ratio of stroma lamellae and end granal membranes increased from the whole membrane system, the efficiency of photosynthetic quantum-transformation decreased. In the 30–15 min and 15–7.5 min. LDC-s the alternation of the light-dark periods inhibits photosynthetic electron stream and weakens CO_2 fixation.

Correlation was sought between the abnormal chlorophyll a/b ratio and the structural anomalies; that is, to what extent does the utilization of light depend on the development of the chloroplast membranes?

One of the characteristic effects of the short periodical illumination is that there is a decrease in the area ratio of the grana.

It is known that there is tight correlation between the production and granal thylakoid number (HORVÁTH and MIHALIK) 1978,

Analysing the results, it could be determined that the damaging effect of the short light-dark periods is firstly manifested in the development of grana having fewer amount of thylakoids, the partition of which is higher.

Destruction of larger degree leads to structural changes in the grana vesicules. This was experienced in the 30–15 min. LDC where the grana vesicules became swollen, then the thylakoids became decomposed.

These morphological alterations also cause considerable decrease in the amount of chlorophylls and carotenoids. The chlorophyll-content shows positive correlation with the number of grana vesicules found in the chloroplasts.

The change in the amount of chlorophyll-b evidences the effect of the treatments the best. Certain plants react in various degrees; in bean and mustard leaves the amount of chlorophyll-b decreases to a large extent, therefore there is an increase in chlorophyll a/b. Outstanding decrease is observable in the amount of violaxanthine, too (AL-SUBAI, 1980).

The considerable decrease in xanthophylls and chlorophyll-b may also be the cause of the relative instability of the LHCP.

The degradation of the chlorophyll-proteins is in connection with the decomposition of the thylakoids (LICHTENTHALER et al., 1981). The chlorophyll-protein complex becomes defected in the fiest place, which is in connection with the PSII. The significant accumulation of the 2–6 thylakoidal grana could be explained by the fact that due to the short and frequent light-dark periods the cation/proton ratio on the stroma plasma and intrathylakoidal space often changes, and differs from the continuous light, resp., which alteration may also affect the chlorophyll-protein complexes participating in the adherence.

The general effect of the short cycles studied by us is that they decrease the amount of starch and are also unfavourable to the accumulation of the total carbonhydrate and dry-matter (MARÓTI and MIHALIK, 1982).

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