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ADAPTATION OF THE MEMBRANEOUS SYSTEM OF BEAN CHLOROPLASTS TO IDENTICAL AND ALTERNATING LIGHT-DARK PERIODS

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Abstract

The growth of Cherokee bean leaves, the degree of dry matter accumulation and the transformation of the membraneous system of palisade chloroplasts were studied:
1. in identical 16—8 hrs, 30—15 min and 15—7.5 min light-dark periods (LDPs) for 5 weeks,
2. as well as in plants grown in LDP changed after the first 3 weeks.

It could be determined that the short-rhythm treatments stimulated the growth of the plants, the development of the leaf and flower initiatives, and increased the area of the leaf.

In the short (30—15 and 15—7.5 min) LDPs identical for 5 weeks the accumulation of dry matter increased for 3 weeks, then decreased compared to the 16—8 hrs LDP.

The plants adapted to various LDPs were further grown in new LDP after 3 weeks (for 2 weeks). At the age of five weeks, the mass of dry matter significantly increased in the case of plants placed from short LDP to long LDP, and decreased in the case of those transferred from long LDP to short LDP.

Positive correlation with dry matter production was found to be the tightest regarding the total membrane/unit cut surface and the partition lengths, as well as the enhancement of thylakoid aggregation. The size of the plasts was in negative correlation with the accumulation of the dry matter.
Key words: light-dark period, dry mass, chloroplast, granum, stacked and unstacked membranes.

Introduction

The development of plants depending on the length of light-dark periods (LDPs) has been known since the beginning of the century. Nevertheless, there are still authors — e.g. Sager and Giger (1980) — according to whom the efficiency of photosynthesis cannot be greater in intermittent light, than in continuous light. We have already reported in several papers that in phytotron, besides identical daily illumination and light intensity, the plants may produce considerably more, or less by applying LDPs of various lengths than in long-day illumination of 16 hrs. According to our studies so far, the 30—15 min light-dark cycle is of transitional character, increasing and decreasing, resp., the light utilization of the plants depending on species, type and genotype. On the contrary, the 15—7.5 min LDP is uniformly unfavourable in respect to plant growth (Horváth and Mihalik, 1978; Maróti and Pataky, 1982; Maróti and Mihalik, 1983; Maróti and Takács, 1983).

In our experiments the daily illumination (16 hrs) and light intensity (32 W/m^2) were identical, but the light-dark periods (LDP) of 2—1, being similar to the long-day illumination, alternated every 30—15 and 15—7.5 min. The 16—8 hrs LDP was regarded as control. These short cycles had significant effect on the development of the plants as well as on the structure of the chloroplast. One of their main effects was that the thylakoid number per granum decreased, but normal grana, stroma lamellae developed (MARÓTI and TAKÁCS, 1983; MARÓTI and PATAKY, 1983), thus basically differed from the light-dark periods of 1/40—1/90 in which cases only primary thylakoids were formed (ARGYROUDI et al., 1976; ARNOND et al., 1976; AKOYUNOGLOU et al., 1978).

The short LDP is similar to the short and long alternations of light and dark in that it firstly changes the light-harvesting complexes and their pigments, respectively (MARÓTI, 1982).

DAVIS et al. (1976) and HORTON et al. (1978, 1980) reported on similar experiments. These authors determined that the transfer from intermittent to continuous light increases the photosynthetic units, resulting firstly in the appearance of the LHC a/b proteins, 12 hours later the differentiation and aggregation of the thylakoid membranes are complete, the concentration of chlorophyll increases and the chlorophyll a/b decreases, resp. The aim of the present paper was to study the effect of the changed LDPs on the development of the plants. Answer was sought to the question, to what extent and how fast are the plants already accommodated to LDP of certain lengths capable of conversion to the new rhythm, and how determinant is the light-dependent prelife?

A main question is whether there is any relationship between the biometry of the membraneous system of chloroplasts and the utilization of light energy. The utilization of energy was followed on the basis of measuring the dry matter production. First the degree of thylakoid aggregation, as well as the relationships between the ratio of the adnated and single membranes and dry matter production were evaluated.

Materials and methods

In our experiments bean plants *(Phaseolus vulgaris* L. cv. *Cherokee)* were grown in phytotron (HORVÁTH, 1972) in the mixture of sand-perlit 1:1 which was humidified at the time of sowing with modified Hoagland nutrient solution in an amount corresponding to 80% of the water capacity (REYSS and BOURDU, 1971). The aliment supply was ensured with 20 ml nutrient solution twice a week and water supply with destilled water daily. F_{29} light tubes were used for illumination. The light intensity was 32 W/m^2; the daily total illumination 16 hrs; the temperature 20 °C±2; and the humidity of the air 50—70%.

1. IDENTICAL SHORT-RHYTHM TREATMENT

One part of the plants were grown in identical LDP from the time of sowing till processing (5 weeks) in which case the plants received three kinds of treatment. The control plants were grown in 16 hrs light and 8 hrs dark period. Two types of short rhytms were applied, in one 30 min light and 15 min dark alternated repeatedly for 5 weeks. In the other short cycle 15 min light and 7.5 min dark alternated.

2. VARYING LIGHT-DARK TREATMENT

In another part of our experiments the plants were transferred to new LDP at the age of three weeks. This was the treatment of varying rhythm. The development of the leaves was followed with attention, the length and width of the primordial and tripartite leaves were measured every second day. The plants were processed at the age of 3 and 5 weeks. The dry mass was measured after drying at 70 °C.

For electronmicroscopic studies samples were taken from the central part of the lateral leaflet of the first tripartite leaf at the age of 5 weeks. The leaf pieces with diameters of 0.5—1 mm were placed in Karnovsky fixative (HALL, 1978) then contrasted with 2% OsO_4 and 2% $KMnO_4$, respectively. The leaves were embedded in Durcupan ACM resin and the sections prepared with Reichert ultramicrotome were stained with Pb-citrate. Pictures were made of the chloroplasts of the palisade cells with TESLA BS 500 electronmicroscope. From the pictures of known magnification the planar size of the plasts, the size and number per unit area of the grana, the htylakoid number per granum (degree of thylakoid aggregation) and the length and ratio of the stacked (partition) and single membrane (stroma lamella, end granal membrane/were evaluated. The length of the membranes and the value of the granal surface ratio were estimated from the whole cut surface of the chloroplasts, also including the starch area. 20—30 plasts were evaluated per treatment. The greatest length and width of the plasts were measured on semithin sections.

Results

1. Effect of identical and varying short LDPs on the dry matter accumulation and leaf growth

At the age of 3 weeks the dry mass of the bean plants grown in 30—15 min and 15—7.5 min LDPs exceeded the dry mass of the plants grown in 16—8 hrs LDP by cc. 10%. Only the initiative of the youngest tripartite leaf appeared during the long

Table 1. The effect of the light-dark periods of different lenght on the dry-matter quantity of 3-week old bean plants.

Light treatment	Dry-matter mg/plant					
	root	stem + petiolus	primordial leaves	l. tripartite leaves	other leaves	total
16—8 hrs LDP	166.7	116.1	165.1	14.4	3.1	466.0
30—15 min. LDC	179.2	129.2	152.3	37.7	5.9	504.3
15—7.5 min LDC	162.5	133.3	126.9	58.0	11.4	492.1

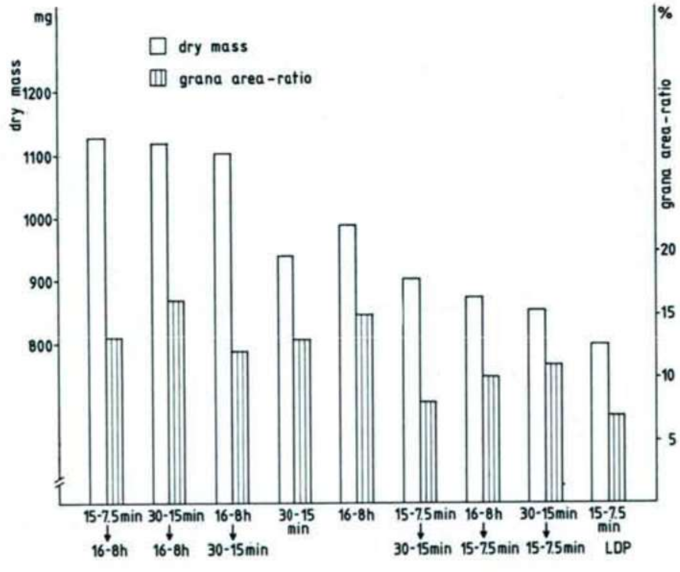


Fig. 1. Changes of total dry mass (mg/plant) and grana area-ratio in 5 weeks old bean plants in identical and alternating LDPs.

day illumination, in the short rhythm these leaves were moderately developed. It was also manifest from the dry mass measurements regarding each plant that the amount of dry mass of the older, developed primordial leaves was less in the short rhythm and that of the young leaf was 2—3 times more compared to the control (Table 1).

The effect emphasizes that there were no buds on the bean plants grown in 16 hrs illumination at the age of 4 weeks, in the 30—15 min cycle violet-coloured buds were found, and in the 15—7.5 min rhythm the beans already flowered.

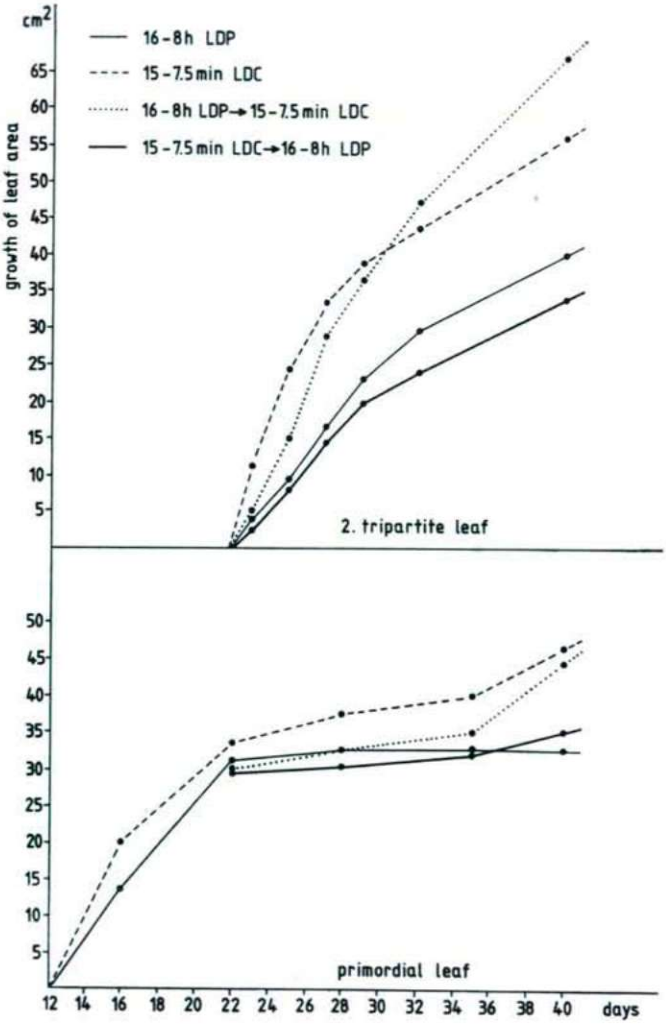


Fig. 2. Effect of identical and alternating LDPs on the area-growth of the primordial and 2. tripartite leaf.

The total dry matter of the plants grown for 5 weeks in identical 30—15 min LDP decreased slightly compared to the control and was about 20% less in the 15—7.5 min LDP (Fig.1).

From the plants grown in varying cycles the dry mass of those increased which grew in shorter (30—15 min and 15—7.5 min) LDPs for the first 21 days and were then transferred to the 16 hrs continuous light for 2 weeks.

Similar increase in dry matter compared to the continuous illumination could also observed when the plants were placed from the 16—8 hrs cycle to the 30—15 min rhythm.

A decrease could be observed in the accumulation of dry matter when the plants were placed from longer LDP to the 15—7.5 min LDP, and also in the case of changing the two short rhythms. The production of the beans grown for 5 weeks in 15—7.5 min cycle was the lowest of all variaton (Fig. 1).

It could be observed from the measurements of leaf growth (Fig. 2) that during the long-day illumination growth rate of the leaves was moderate, growing less quickly. After transfer the new rhythm had less effect on the growth of the older leaves. New LDP only merely affected the development of the primordial leaves, even after transfer they grew at the rate characteristic to the original rhythm. The young tripartite leaf rapidly accommodated to the growth rate characteristic to the new LDP.

Transfer from longer to shorter cycle resulted fast development regarding the young leaves, e.g. the growth of the leaf area was 5 times greater in the case of transfer from 16—8 hrs to 15—7.5 min cycle, than in the case of plants grown for 5 weeks in 16 hrs light.

2. The effect of identical and various LDPs on the structure of the chloroplast

There was an increase in the size of the chloroplasts of the palisade parenchyma on the effect of the short cycles, and even a change was detectable in the shape of the plasts; they became elongated, flattened (Plate I). In control leaves the length of the plasts was 5.5 μ and their width 3.5 μ. On the effect of short rhythm treatment their length increased to 7.5—8 μg and their width to 4 μ. The cut surface of the chloroplasts of plants grown in long-day illumination was occupied by starch in 15—20%, the membraneous system was found in the peripheral parts (Plate I).

The characteristic effect of the short LDPs on the structure of the plasts was also expressed by the lack of accumulation of assimilative starch. The amount of primary starch was also similarly low (1—2%) in the case of transferred plants where the production showed a decrease compared to the control (Plate IV). In the case of plants placed from short rhythm to 16 hrs continuous light, the considerable amount of dry mass was accompanied by high amount of assimilative starch (Plate III). The number and size of grana, as well as the changes in granal surface-ratio were also studied. The amount of grana found on the entire cutsurface was the largest in the case of the shortest cycle. It was also of similar high value in the plants transferred from 15—7.5 min LDP to 16 hrs illumination. In the leaves grown at continuous light the total grana amount was averagely 15%. The 30—15 min LDP treatment also was close to this value. The 15—7.5 min rhythm decreased the quota of grana by more than 50% (Fig. 1).

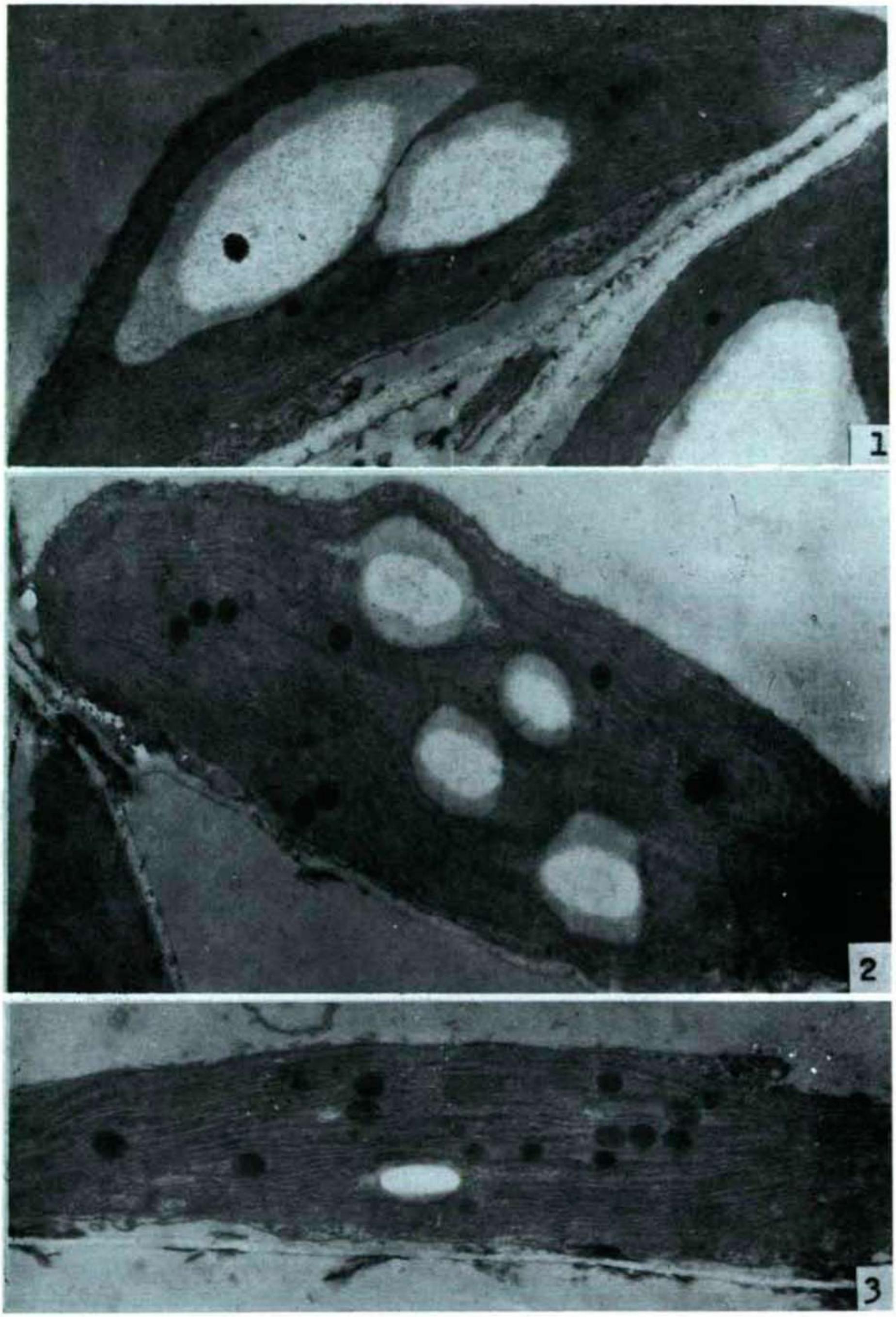
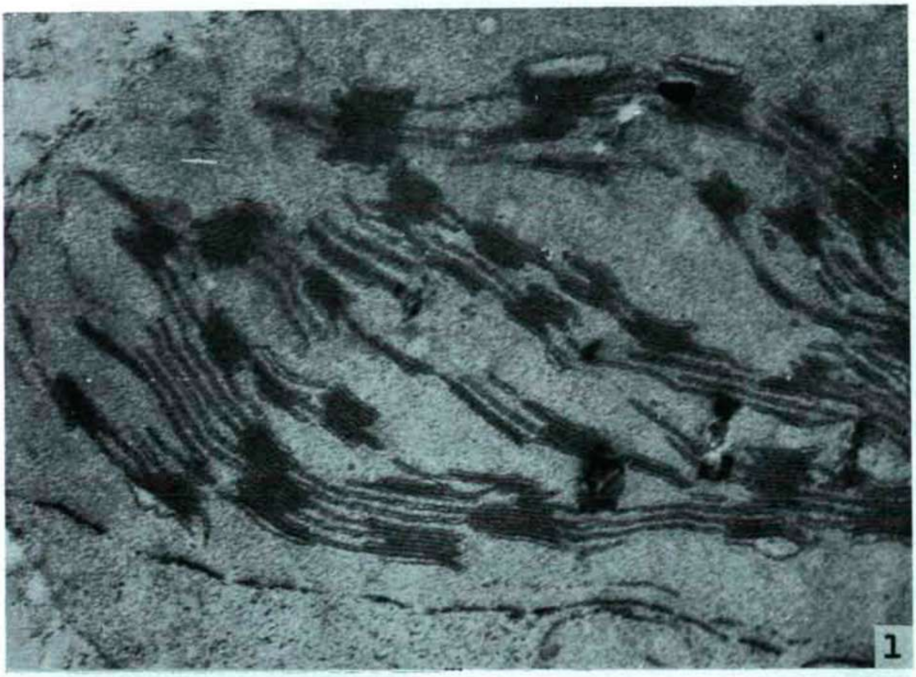


Plate I.

1. light-dark cycle 16—8 hrs (25 000×)
2. light-dark cycle 30—15 min (25 000×)
3. light-dark cycle 15—7.5 min (25 000×)



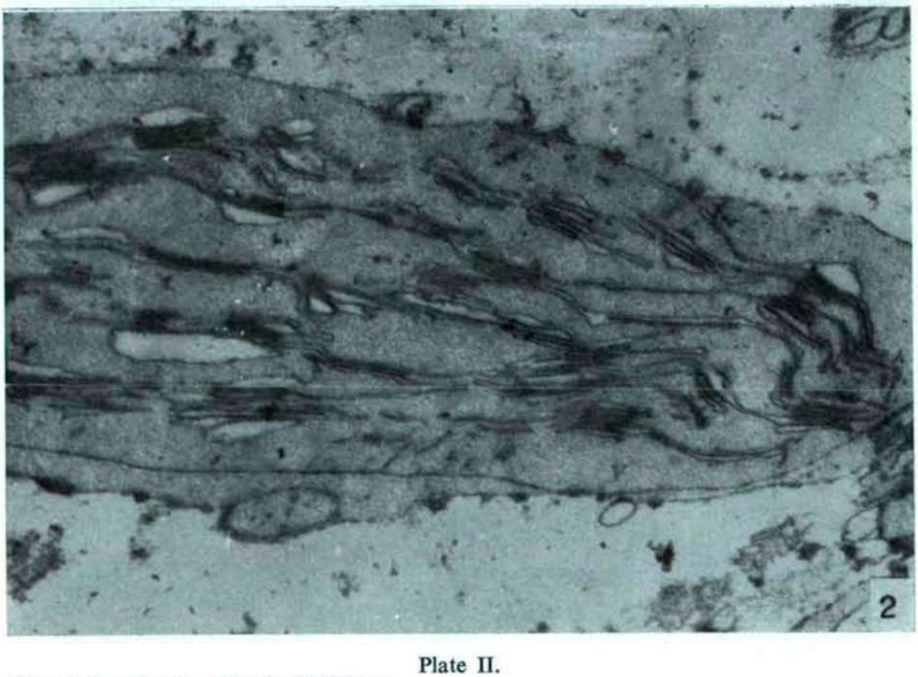


Plate II.

1. light-dark cycle 15—7.5 min (35 000×)
2. light-dark cycle 15—7.5 min → 30—15 min (35 000×)

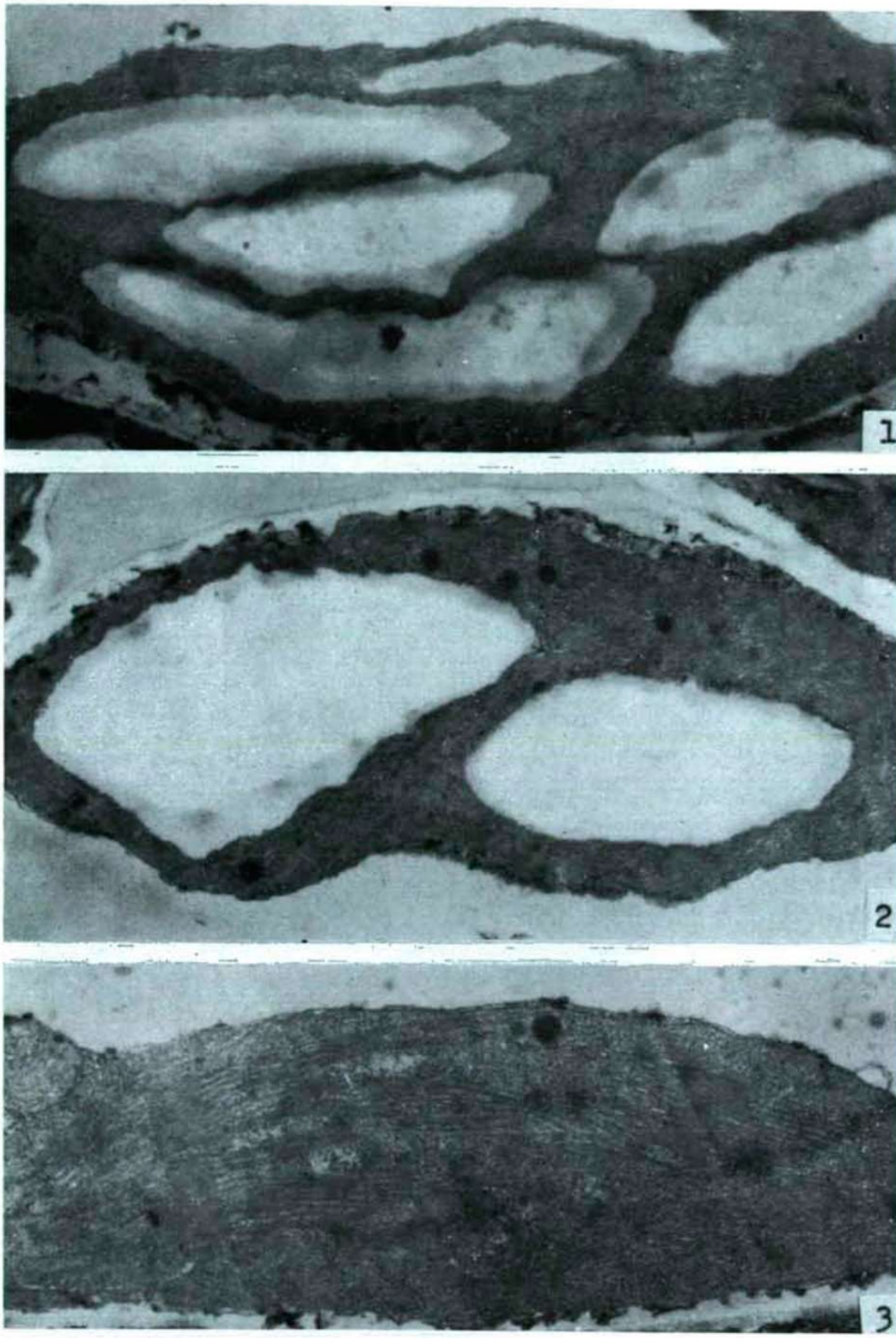


Plate III.

1. light-dark cycle 15—7.5 min → 16—8 hrs (25 000×)
2. light-dark cycle 30—15 min → 16—8 hrs (25 000×)
3. light-dark cycle 16—8 hrs → 30—15 min (25 000×)

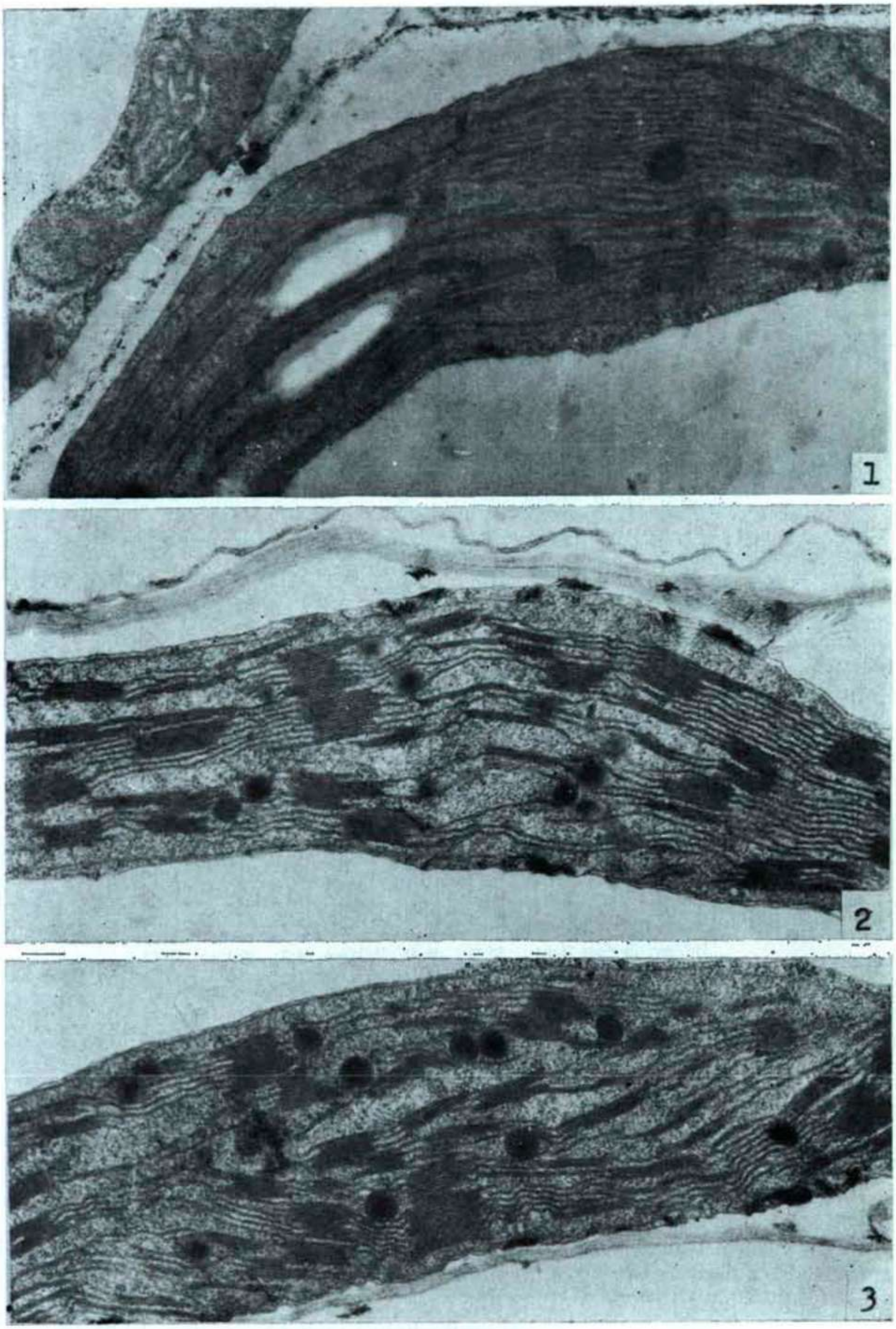


Plate IV.

1. light-dark cycle 16—8 hrs → 15—7.5 min (25 000×)
2. light-dark cycle 30—15 min → 15—7.5 min (25 000×)
3. light-dark cycle 15—7.5 min → 30—15 min (25 000×)

On the basis of thylakoid aggregation, grana were separated into three groups: grana composed of 2—9 (few); 10—21 (average); 22—35 (many) thylakoids (Fig. 3).

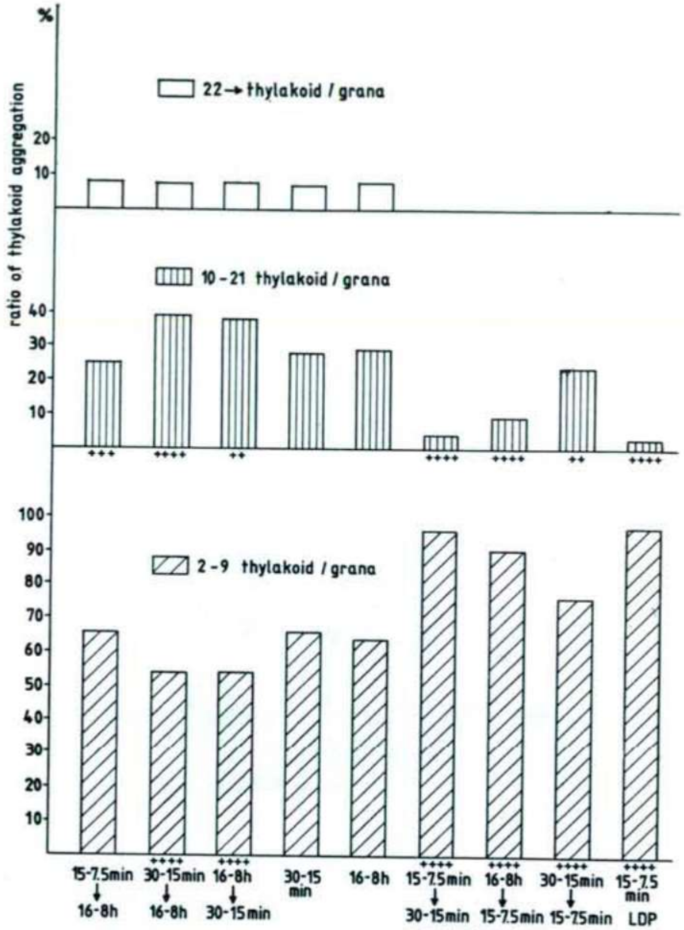


Fig. 3. Effect of identical and alternating LDPs on the degree of thylakoid aggregation. Significance: P=10% +; P=5% ++; P=1% +++; P=0,1% ++++.

In the plasts of leaves grown in long-day illumination and 30—15 min LDP the grana standing of 10—21 and 22—35 thylakoids occurred in about 40%.

In the 15—7.5 min LDP grana stacked by 2—9 thylakoids dominated, their frequency was 98%. Grana made up of high columns did not develop.

In the case of transferred plants where the production of dry matter increased, there was also a high frequency of medium and large-sized columnar grana developed by the tightly stacked thylakoids. In the case of bean plants transferred from one short cycle to another, and from continuous light to the 15—7.5 min LDP, respectively, the degree of thylakoid aggregation became slighter parallel with the decrease in production, and grana composed of 20—30 thylakoids were not observable either.

The partition of the multithylakoidal grana was short, their height per width ratio was high. The partition surface of the grana discs increased with the decrease in thylakoid aggregation. The conformation of the thylakoids showed considerable change on the effect of the 15—7.5 min short cycle. In one part of the plasts the grana. intrathylakoidal spaces became swollen, expanded. The loculi of the end discs dilated into wide sacks at many places. Similar dilatation could also be observed in respect to the stroma lamellae. Many vesicules were found at the edge of the stroma lamellae. These dilating processes were not characteristic to every plast membrane, but these manifestations proceeded in about half of the studied chloroplasts, in smaller-higher degree (Plate II).

Table 2. Effect of identical and alternating LDPs on the organization of the thylakoid membranes of the palisade chloroplasts in the 1. tripartite leaf.
Significance: P=10%+; P=5%++; P=1%+++; P=0,1%++++

Light treatment	Number of grana/chloroplast section area	Total lamellar material μ/μ^2	Partition lenght μ/μ^2	Stroma lamellae μ/μ^2	End granal membrane μ/μ^2	Proportion of partition to total lamellar material	Proportion of stroma lamellae to total lamellar material	Proportion of end granal membrane to total lamellar material
16—8 hrs LDP	39	30	18	8.6	3	61	28	11
30—15 min ↓ 16—8 hrs	37	27	15	8.1	3.3	57	30	12
15—7.5 min ↓ 16—8 hrs	56	27	16	7.2	3.4	60	27	13
16—8 hrs ↓ 30—15 min	32	21++	13++	6.7+	2.1+	59	31	10
30—15 min LDC	38	21++	12+++	6.3+	2.5+	57	30	12
15—7.5 min ↓ 30—15 min	34	16++++	7.5++++	5++	3.3	47	33	20
30—15 min ↓ 15—7.5 min	31	17+++	9++++	5++	2+	55	22	13
16—8 hrs ↓ 15—7.5 min	34	19+++	9++++	6.7+	3.6	47	34	19
15—7.5 min LDC	54	11+++	5++++	3+++	3.4	44	26	30

The ratio of the stacked and single membranes was also studied and the membrane length per unit area was evaluated (Table 2). Answer was sought how the membrane organization of the chloroplasts changed if the plants were grown further in another LDP.

The 9 variants could be divided into 2 groups, from the viewpoint of light utilization, taking the effect of the treatments into consideration.

1. High accumulation of dry matter could be observed in the case of plants grown in 16 hrs illumination and 30—15 min LDP, as well as in those transferred from short rhythm to continuous light. In these treatments the quota of the stacked membranes was around 60% from the total membranes. The partition heights calculated per unit area were also the greatest in these plasts. The total membrane-length per 1 μ^2 was of high value, around 20—30 μ (Table 2).
2. In the other group, where the efficiency of photosynthesis showed a decrease, the lamellation of the plasts as well as the total membrane lengths per unit area decreased to about the half and there was also a decrease in the quota of the partitions. The quota of unstacked membranes from the total membranes was high — 50—60% — in the 15—7.5 min LDP and almost the same result was obtained by transfer from 16 hrs illumination to 15—7.5 min rhythm, as well as by exchange of the 15—7.5 min and 30—15 min cycles.

   The slightest change could be observed in respect to the stroma lamellae, their quota from the complete membrane length merely changed on the effect of the various treatments. The degree of lamellation and the partition heights per unit area were the lowest in the 15—7.5 min cycle. On the contrary, considerable increase was detectable in the ratio of the end granal membrane (to the triple). This change could be explained by the increase in granum number and the decrease of thylakoid aggregation.

Discussion

The dry mass of the 3 weeks old plants surpassed that of the control plants in the shorter rhythm treatments. This increase in production was ensured by the more intensive growth of the tripartite leaves which appeared and developed at an earlier time-point than in the long-day illumination.

It was also striking from the dry mass measurements that the short rhythms decreased the dry mass of the older, developed primordial leaves of the bean plants, and enhanced the growth and accumulation of the young leaves.

The total dry mass production of the plants grown for 5 weeks in identical LDP was lower in the short LDP than in the 16 hrs illumination.

The decrease in dry matter accumulation could be explained by the fact that although the area of the leaves and the height of the plants increased, the stem and leaf lamella were thin, the sclerenchymaelements were few and there was higher amount of water in the leaves. Our earlier studies have also determined that the epidermal cells and the number of stoma per unit area increase on the effect of short cycles. There is negative correlation between the dry mass and the cell number (MARÓTI et al., 1981).

MARÓTI and MIHALIK (1983) connect the faster development of the young leaves and the higher cellulose/starch ratio of the leaf in the short LDP with the enhanced carbohydrate translocation.

New rhythm applied at the age of 3 weeks had hardly any effect on the growth of the older, primordial leaves, the light conditions were determinative on their growth in which they developed. Therefore prelife remains determinant throughout the course of ontogenesis.

The tripartite leaves finished their growth and developed, resp. in the new rhythm, thus they quickly accommodated to the growth rate characteristic of the new LDP.

The short LDPs enhanced the growth of the plants at young age, and the leaf gaining advantage of growth in such way developed for longer period with more moderate growth intensity when transferred to continuous light, also giving the highest value of dry mass accumulation. There were differences in the manifestation of this effect according to cycle-length. The exchange of the 30—15 min and 16—8 hrs LDPs firstly increased the dry matter accumulation of the vegetative organs, while the combination of the 15—7.5 min and 16—8 hrs LDPs was more favourable to the development of the reproductive organs, accelerating their growth and ripening.

On the basis of our results relationship was searched between the dry matter production and the chloroplast size, starch content, and structure of the inner membrane.

It was determined that in the palisade cells, the size of the plasts was in negative correlation with the degree of dry matter accumulation.

Primary starch was not found accumulated in the chloroplasts of the plants in the short rhythms.

In their survey, GIFFORD and EVANS (1981) emphasized that in the literature of the recent years 50—50 such results were found according to which photosynthesis was hindered in the leaf by assimilative end products and this was not regulated by such a simple mechanism, resp, but had more profound causes. The results of MARGÓCZI (1984) demonstrated that the soluble sugar and starch level in the maize leaves decreased on the effect of illumination of shorter rhythm. The decrease in starch level experienced in the case of shorter rhythms was in good correlation with the lower assimilative starch content found in the chloroplast.

The photosynthetic efficiency and the amount of carbohydrates showed positive correlation. The more the soluble carbohydrate in the leaf, the higher the dry mass. When short-rhythm treatment increased the dry mass of the leaves, the higher production was not based on the fact that the amount of soluble carbohydrate decreased in the dark as the result of translocation, since the dry mass was the greater there where it was found in higher amount in the leaf and where the amount of soluble sugar decreased to a smaller degree (MARÓTI and MIHALIK, 1983; MARGÓCZI, 1984).

In the short LDP the number of grana increased but the grana area ratio decreased which on the one hand was the result of the grana occupying smaller part of the plasts having larger cut surface. On the other hand, there was also a decrease in the size of the grana. Increase in stroma-plasma could be observed. The majority of the PS I. particles were found in the unstacked membranes (ARNTZEN et al., 1969). There are two possibilities for the accumulation of the single membranes: the increase in stroma lamellae and the grana terminal membrane surfaces, respectively (MARÓTI and GÁBOR, 1976). In the case of beans, in short LDPs the latter was manifest with the decrease in thylakoid aggregation.

The considerable increase in the amount of grana standing of few thylakoids could be explained by the fact that due to the short and frequent dark periods the cation/proton ratio in the stroma plasma and the intrathylakoidal spaces frequently changed and was divergent from the continuous light, resp.

It has been demonstrated (MARÓTI, 1982) that in the case of plants where besides strong illumination the value around pH 5 forms slower in the loculus, it is firstly the pigments (chlorophyll-b, neoxanthin) of the light-harvesting complexes (LHC) which become decomposed. The degree of stacking and the amount of LHC and chlorophyll-b, respectively, are in positive correlation (GEROLA, 1981; LICHTENTHALLER et al., 1981).

On the basis of the above mentonied things it is presumed that one of the important regulators of the degree of thylakoid aggregation is the exchange of H^+/Mg^{2+} between the two sides of the thylakoid membrane. Several authors have shown that photosynthesis is hindered by the decrease in stroma Mg^{2+} and pH (LATRA and KELLY, 1978; WERDAN et al., 1975).

In short LDP the low light intensity (32 W/m²) and the frequent dark periods hinder the formation of pH gradient necessary for the gaining of energy of the thylakoids. It is presumed that this is why the thylakoids become swollen and the stroma relatively acidify, resp.

It is known that ATP formation strongly depends on the pH, its maximum being at pH 8.3 (CHERYL and GOULD, 1980).

In our experiments the considerable amount of dry matter found in the case of LDPs favourable to growth was accompanied by the high value of the stacked membranes (Fig. 4). The correlation coefficient value was 0.81 which was significant at P=1%.

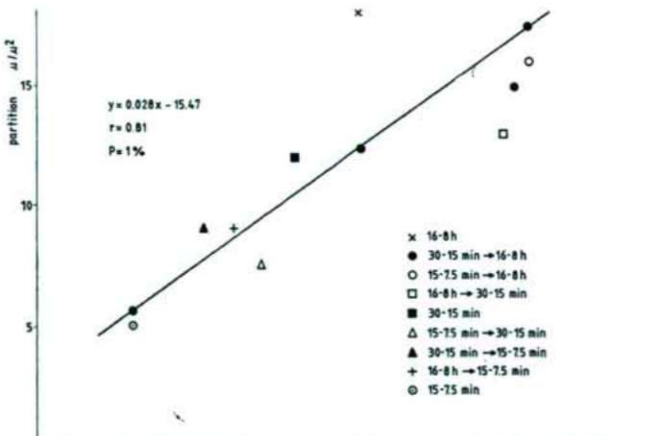


Fig. 4. Correlation between the total dry mass and stacked membrane lengths per unit area.

The changes in grana area-ratio and dry mass were nearly similar, however, no tight positive correlation was found between them (Fig. 1).

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