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THYLAKOID AGGREGATION AND PIGMENT RATIOS IN THE SPONGY AND PALISADE PARENCHYMAS[1]

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Abstract

We drew conclusions about the localization and the role of the photosystems in the spongy and palisade parenchymas from the thylakoid aggregation and pigment ratios. The spongy and palysade parenchymas were isolated from the leaves of the species investigated. From a part of tissue specimens the pigments were determined, other parts were studied with electron-microscopic methods. On the basis of the fine-structure analysis of chloroplast membranes adn pigment measurings we have established that:

1. In the spongy p. chloroplasts the complete length of the partition per grana is in every case larger, and the chlorophyll a/b ratio is smaller, than in the palisade p. chloroplasts. The measure of thylakoid aggregation is in a negative correlation with the chlorophyll a/b ratio.
2. We suppose by reason of the literary data and our own results that photosystem I is localized in the terminal membrane, the stroma lamellae, at the surface of partitions from the loculi, and photosystem II, however, interthylakoidally at the external surface of the membrane.
3. Photosystem I is enriched in the palisade p. chloroplasts, and photosystem II in the spongy p. chloroplasts. The ratio of photosystem I may increase by enlarging the surface of stroma lamellae and reducing the degree of thylakoid aggregation.
4. On the basis of our results we confirm and, in other respects, keep on developing Arnon's opinion (2), according to which the regulation of the products of photosynthesis (the synthesis of soluble carbohydrate, starch, cellulose, protein, lipoid matters) is realized, in the last analysis, through the dynamic change in the ratio of photosystems.

Introduction

The final aim of the electron-microscopic investigation of chloroplast is to localize the processes of photosynthesis and connect them with one another. As the environment is to be studied in a macromolecular way, the investigations of ultrastructure are to be completed with measruings of other an character, as well. In organizing the chloroplast membrane, the pigments have a functionally prominent significance. The spongy and palisade parenchymas were earlier isolated from the leaves of several species, then the quantity of the single chlorophylls and carotenoids was determined. We suppose, on the basis of the pigment ratios, that:

— In the palisade parenchyma of the leaves developed, the ratio of photosystem I is higher, in the spongy parenchyma, however, that of photosystem II.

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[1] A part of the paper was read — MARÓTI (1974) — in Poznan (COMECON Conference, Theme I—18.2).

- In the spongy parenchyma Hill's reaction, the non-cyclic photosphosphorylation and CO_2 fixation prevail out in the palisade parenchyma the cyclic photophosphorylation prevails.

Taking into consideration the above-mentioned facts, on the basis of the ultrastructure of chloroplast, we should like to prove the separation of photosystems in the mesophyll and the change in their ratio.

At the chloroplast investigations so far, the leaf was considered as homogeneous without distinction according to the origin of chloroplast from one or another tissue layer. We are demonstrating on the basis of a study of the pigment ratios that the chloroplasts form a heterogeneous ensemble in the leaves. There were comparatively few researchers dealing with the connection between the fine structure of chloroplast and the pigment ratios.

REGER and KRAUSS (1969) demonstrated in the case of Chlorella algae that the ratio of chlorophyll a/b, the quantity of dry matter, the size and number of starch granules are increased by a stronger light intensity but, at the same time, the quantity of chlorophylls and the degree of thylakoid aggregation decrease.

According to REYS and BOURDU (1970), HIRSCHAUER *et al.* (1971), in the case of *Lolium multiflorum* the ratio of chlorophyll a/b is increased and the thylakoid numbers per grana are decreased by a short photopeirodic illumination.

It was demonstrated by WOO *et al.* (1970) in the case of C_4 plants that the product of multiplying the number of partition per the chloroplast area of mesophyll and bundle sheat with their total length is in inverse ratio to the ratio of chlorophyll a/b. In respect of the part of chlorophyll b in photosystem II the opinions differ. In Smith's opinion (1954), the presence of chlorophyll b is non-essential to the development of oxygen. A similar result was achieved by GOODCHILD *et al.* (1966) who established that chlorophyll b is a not indispensable component of the grana of higher-class plants. The stability of grana is, however, damaged by a lack in chlorophyll-b.

FALUDI-DÁNIEL *et al.* (1968, 1970) demonstrated that besides chlorophyll-b, carotenoids play, a very important part in the formation of grana and the stability of membranes. According to FALUDI-DÁNIEL and NAGY (1972), photosystem II functions not only in grana, and the Hill activity may even be higher in plastids containing no grana than in the normal lamella-system with grana.

The opinion of van HOMANN and SCHMID (1967) is, to certain extent, oppossed to the ones above. In a study of tobacco mutants, they demonstrated that the full activity of photosystem I might take place in isolated thylakoids, as well. To the activity of photosystem II, however, a close adhesion of at least seven thylykoids is necessary.

We have compared the literary results achieved by biochemical, cytochemical methods with our own electron-microscopic and pigment-investigations, completing in this way the dynamic connection and localization of the photosystems with new data.

Material and Method

Ww have used for our investigations the developed young leaves of the barren shoot of *Hedera helix* L., those of *Nuphar luteum* L., and *Nonea lutea* (Desv.) DC. Detaching the spongy parenchyma from the palisade one, we cut 0.2 to 1 square mm pieces from these tissues. We fixed the matter in 3 per cent glutaraldehyde, in a buffer of 0.05 M $KHPO_4$—$NaHPO_4$ and saccharose content (pH=7.2) at 24 °C for three hours. Then we washed the tissue speciemens in the above buffer, refixed them with 1 per cent O_sO_4 in a buffer of 0.05 M potassium phosphate for three hours. We washed them again and dehydrated in an ascending alcohol series and propylene oxide, treating them in the meantime with uranyl acetate in 70 per cent alcohol. After dehydrating the matter, we embedded it into a Durcupan-ACM mixture. The section was carried out with Reichert's OMU_2 ultramicrotome. The sections of silver and golden colour were made contrastive by means of lead citrate. The photographs were prepared with a TESLA BS—500 electron-microscope.

The matter was embedded three different times. Measurings were carried out at 8 to 10 chloroplast recordings for each species and tissue (ca 120—150 grana, on 1 to 2000 thylakoids).

Results and their evaluation

1. Terminology of the fine structure of chloroplast and localization of photosystems

In spite of the unifying tendencies — Weier *et al.* (1962, 1967), Menke (1962) — the nomenclature of the chloroplast ultrastructure is not unambiguous. We deem therefore necessary to determine the concepts used by us.

1. Membrane: the electron-microscopically single-layer, so-called chloroplast "unit" membrane consists — according to Frey—Wissling and Steinmann (1953), Menke (1962, 1963), Weier adn Benson (1965, 1967) — of one layer of the globular lipoprotein membrane sub-units of 40—155 Å diameter.
2. The lamella is a double membrane consisting of parts close to each other and belonging loosely together. Instead of stroma thylakoid the name stroma lamella is generally used today. Between the two stroma membranes a stromal channel Nir and Pease (1973) — is formed, with some matter of hydrophilous nature between them (Weier and Benson (1965)). At the internal surface of the stromal membrane only the photochemical system I is localized. Nir and Pease (1973), Gasanov and French (1973).
3. Thylakoid is the structural unit of the photosynthetic lamella-system, consisting of a close double membrane: Menke (1962). The thylakoid membrane encloses a loculus.
4. Grana are formed by a close association of the external surfaces of two or more thylakoids. In the course of the appreassed of thylakoids, the two membranes of the adjacent thylakoids and the interthylakoidal gap are together forms a partition: Weier and Benson (1965). According to Nir and Peace (1973) the partition is about 130 Å broad, of which the interthylakoidal space of hydrophilous nature is 40 Å. Homann and Schmidt (1967), Woo *et al.* (1970), Nir and Peace (1973) demonstrated that on the external surface of the thylakoid membrane, in the partition, photosystem II was localized, and on the internal surface, towards the loculus, the photochemical system I. In our paper we reach to the conclusion that photosystem I is separately localized not only in the stroma lamellae but in the end granal membranes, as well.

In the case of the grana consisting of some thylakoids the end granal membrane per partition ratio is: 2 to 1, and in case of the multilamellar grana: 0.5 to 0.05.

In the course of analysing the fine structure of chloroplast, we measured: *a)* the thylakoid number per granum; *b)* the average length of the partition; *c)* the total length of the partition per grana; *d)* the length of the partition and stroma lamella on the unit surface; *e)* the percentage distribution of the thylakoid aggregation.

We have supposed by reason of the literary data and our own results that the photosystems are localized in the followign membranes:

1. At internal surface of the end granal membrane: PS—I.
2. At internal surface of the stroma lamellae: PS—I.
3. In the partition, at internal surface of the grana thylakoid, towards the loculus: PS—I.
4. In the partition interthylakoidally, at external surface of the membrane: PS—II.

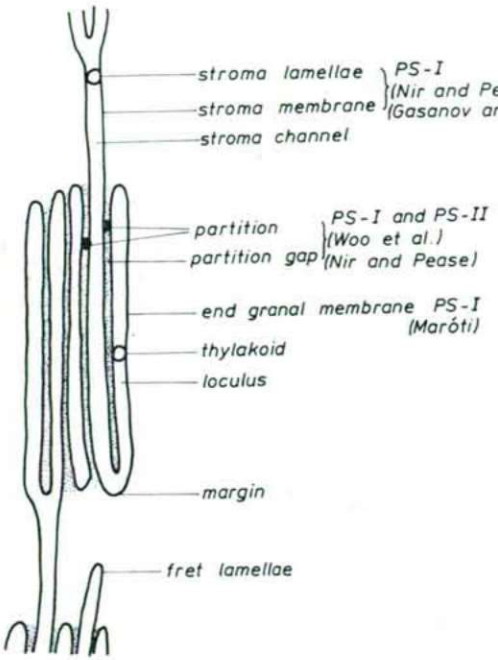

Fig. 1. Nomenclature of the chloroplast and the supposed localization of the photosystems

2. Characterization of the ultrastructure of chloroplasts

a) *Hedera helix* L.

The most chaarcteristic peculiarities of the chloroplasts of the spongy parenchyma (s. p.) (Plates: I/1; I/2; II/1) are the broad, lamellar macrograna turning into one another. The grana thylakoid margins do not overlap one another. The partition number, partition length per grana considerably outnumber, resp. exceed those of

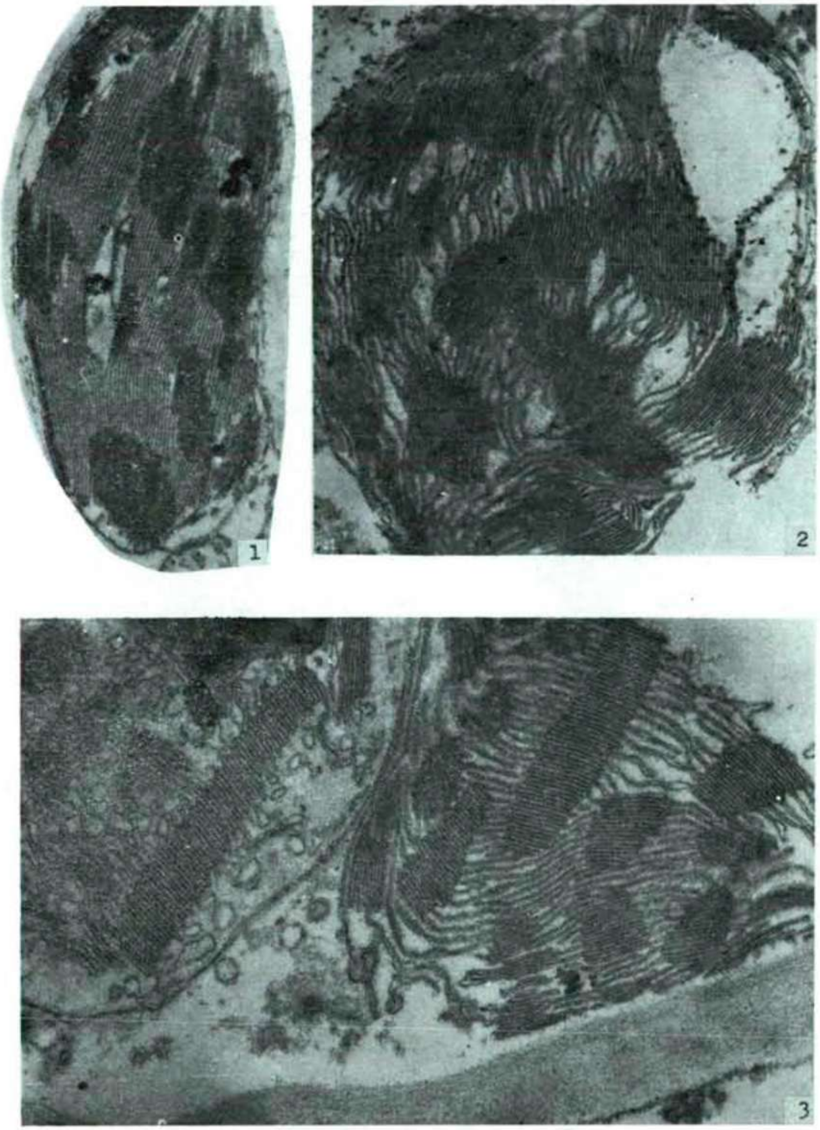

Plate 1

1. *Hedera helix*, spongy p. chloroplast. The plastid membrane is completely filled up with stroma lamellea. "Sham" loculi are formed in interlamellar way. x20.000.
2. Chloroplast of spongy parenchyma of the leaf of Hedera helix. In the plastid broad, macrograna are to be seen, going over to one another. The partition per stroma thylakoid ratio is larger than in the palisade chloroplast. x29960.
3. Chloroplast details from the palisade parenchyma of Hedera helix. The grana form long "palisades" and stand out in sharp contrast to the stroma thylakoids. The partition per stroma thylakoid ratio is smaller than in the spongy chloroplasts. x29960.

The sections were made with $KMnO_4$ contrasting.

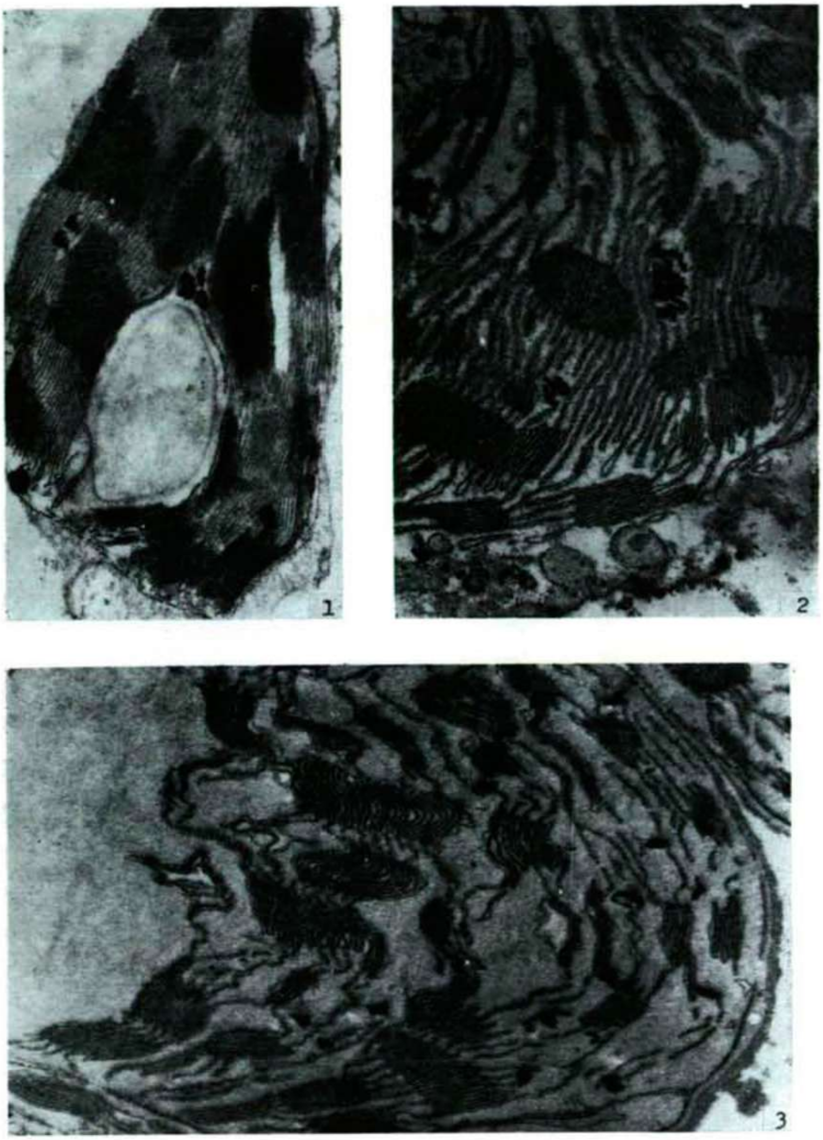

Plate 2

1. *Hedera helix*, spongy p. Chloroplast. Broad macrograna, large starch granules are to be found in plastids. x20 000.
2. Palisade parenchyma chloroplast from the leaf of Hedera helix. The partition per stroma thylakoid ratio is larger than in the spongy parenchyma. x29960.
3. Chloroplast from the palisade parenchyma of Nonea lutea. The stroma thylakoids and grana terminal membranes are of greater number than in the spongy chloroplasts. x29960.

The sections were made with $KMnO_4$ contrasting.

the chloroplasts in the palisade parenchyma. The stroma thylakoid count falling to the unit area is lower than in the palisade chloroplasts. The membrane system often fills up the chloroplast in its entirety. Under the chloroplast membarne, therefore, the peripheral zone of the stroma plasm is lacking. The peculiarity of the stroma lamellae that the membranes are closely adhesive, hardly any loculus being visible between them, is different from the other chloroplast. Between the stacks of the accumulated stroma thylakoids some interlamellar loculi can be formed, being in fact sham loculi. In the s. p. chloroplasts the large starch granules are frequent. (Cf.: Table 1.)

In the palisade parenchyma (p. p.) chloroplasts (Plates: I/3; II/3) the size of grana is changing. Some grana consisting of several thylakoids can be observed in almost every chloroplast. The grana-thylakoid margins occur closely above each other. The average length of partitions is nearly half of those existing in the spongy-parenchyma chloroplasts. The full length of the partition per grana is considerably shorter than in the s. p. chloroplasts. The count of stroma lamellae on the unit area is greater than in the s. p. chloroplasts. Between the stroma lamellae the real loculi can be seen well. The stroma thylakoid often gets blistered (supposedly in the course of embedding) (Cf.: Plate I/3).

In the p. p. chloroplasts there are sometimes present tiny starch granules, as well. The difference between species, is also shown well by the fine-structure analysis (Cf.: Table 1).

b) *Nonea lutea* (DESV.) DC.

In the spongy parenchyma (s. p.) chloroplasts (Plate: III/1) the membranes are organized for the most part into grana. The average thylakoid count per grana is: 6.5. That is only slightly higher than in the p. p. chloroplasts where this value is 5.6. The length of the stroma lamellae on the unit area differs considerably from that of the p. p. chloroplasts. In the spongy parenchyma chloroplasts the starch granules of various size can often been observed. The difference of chloroplasts in the two tissues of mesophyll is well-shown by the analysis of the ultrastructure of chloroplasts (Cf.: Table 1).

The most characteristic peculiarities of the palisade parenchyma (p. p.) chloroplasts (Plates II/3; III/2—3) are: the heterogeneous granum size and form, as well as the large number of the stroma thylakoids. The grana consisting of a few thylakoids are long (cf.: Plate III/2—3) and their course is wavy. The grana terminal membranes have rugous surfaces, often with blisters. In this way, enormous loculi are formed. The partition of the multithylakoidal grana is short and, consequently, the average partition length per grana is shorter than in the spongy parehchyma chloroplasts (cf.: Table 1). In the chloroplasts no starch granules were found. In the palisade parenchyma chloroplasts the length of the stroma thylakoids on the unit surface is almost double that in the s. p. chloroplasts.

c) *Nuphar luteum* (L.) SM.

The most characteristic peculiarities of the spongy parenchyma (s. p.) chloroplasts (Plates: III/4; IV/1) are: the multilamellar macrograna, the granular stroma plasm, and the swelling of loculi. It may even be supposed on the basis of the shape of the interthylakoidal spaces that are visible in the pictures that these are the positions of the starch granules dropping out at cutting. It is to be observed, however, that the grana terminal membranes, too, get often blistered and that is in opposition to the supposition that these places are all the position of starch granules. As a result of

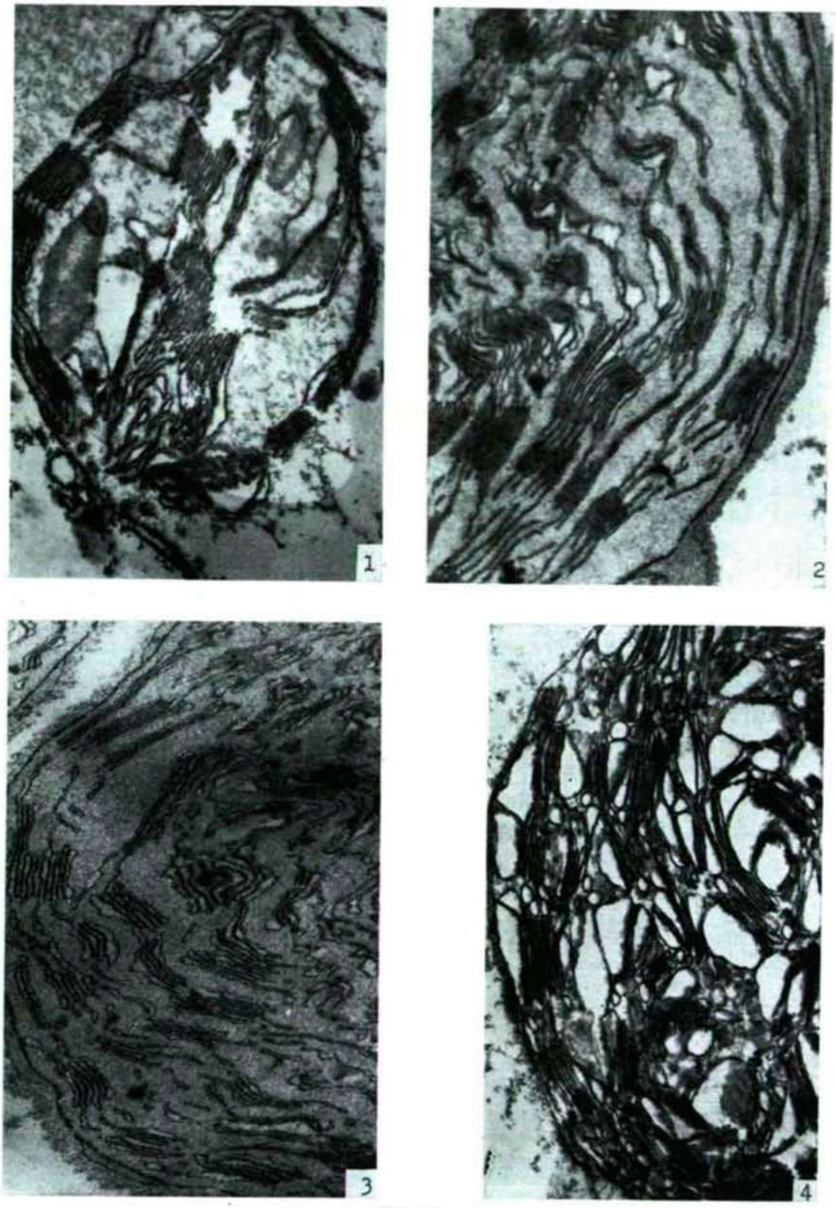

Plate 3

1. Spongy parenchyma chloroplast from the leaf of Nonea lutea. In the plastid starch granules are to be observed, a part of thylakoids are organized into grana, there are onyl few stroma thylakoids. x21400.
2. Chloroplast from the palisade parenchyma of Nonea lutea. Among the multithylakoidal grana of short partition there are several grana consisting of a few thylakoids and having long partitions, as well. The numbers of stroma thylakoids are considerable, too. x29960.
3. *Nonea lutae*, palisade p. chloroplast. The numbers of stroma lamellae and grana terminal membranes are more than in the spongy p. chloroplasts. Blistering and crinkling of the grana terminal membranes are frequent. x29960.
4. Spongy parenchyma chloroplast from the leaf of Nuphar luteum. Loculi, particularly in the grana terminal thylakoids, are strongly swollen. x29960.

The sections were made with $KMnO_4$ contrasting.

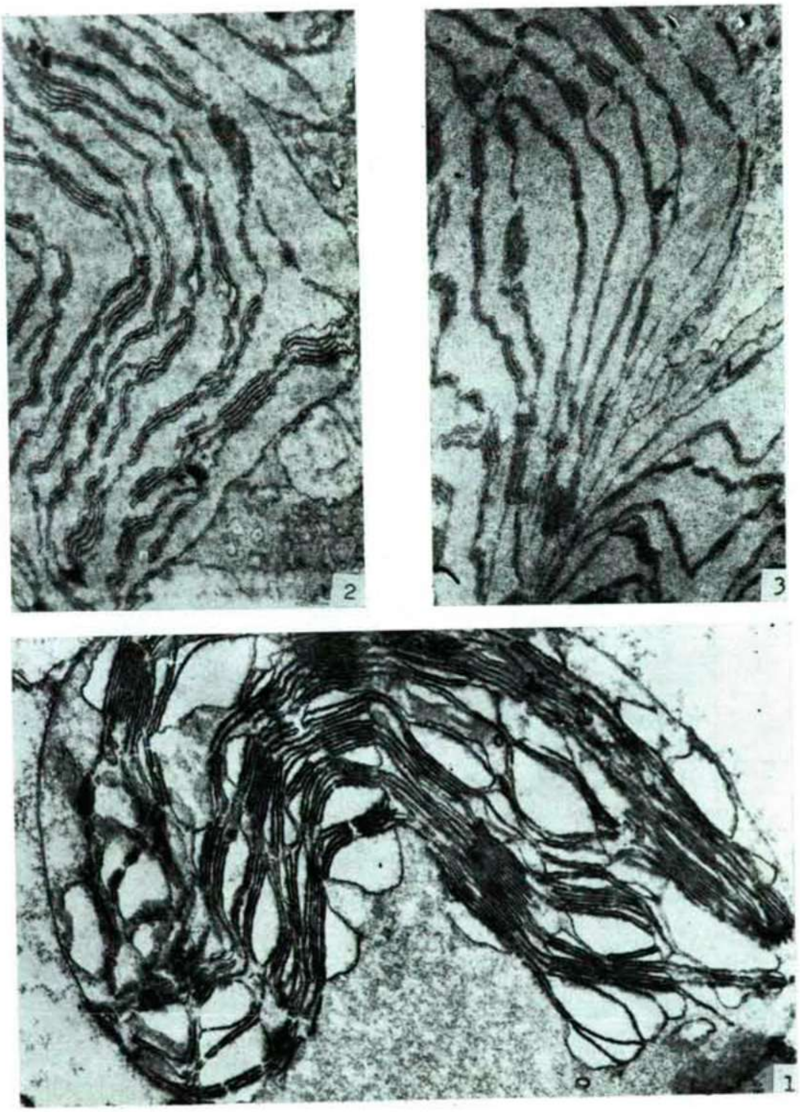

Plate 4

1. Spongy p. parenchyma from the leaf of Nuphar luteum. Grana are consisting of several thylakoids. In the s. p. chloroplasts there are many swollen loculi. x29960
2. Chloroplast detail from the palisade parenchyma of Nuphar luteum. The terminal membrane per partition ratio is much larger than in the spongy p. chloroplasts. x29960.
3. Detail of a palisade parenchyma chloroplast of Nuphar luteum. Several grana consist of only two or three grana thylakoids. In the grana consisting of a few thylakoids the partitions are long, in those consisting of more thylakoids, however, they are short. The course of lamellae is wavy, supposedly as a consequence of non-preparation. x29960.

The sections were made with $KMnO_4$ contrasting.

the grana terminal membranes getting blistered, the stroma plasm is divided into spaces. In the stroma plasm, besides the large electron-spreading globules, there are to be found several osmiophilous granule stacks (cf.: Plates IV/1, III/4). These are probably polyribosomes. It is a remarkable peculiarity of the s. p. chloroplasts wich is different from the other species that there are. more stroma lamellae on the unit surface than in the palisade parenchyma chloroplasts (Cf.: Table 1).

In the palisada parenchyma (p. p.) chloroplasts (Plates IV/2, 3) the grana with long partition and consisting of 2—3 thylakoids are frequent, and the grana terminal membranes become rugous, blistered. The p. p. chloroplasts have grana of characteristically heterogeneous sizes and shapes. The partition falling to an average granum is longer than in the s. p. chloroplasts. That seems to be a species peculiarity. The p. p. and s. p. chloroplasts were embedded in a completely identical way. A considerable blistering of loculi could not be observed, after all, in the p. p. chloroplasts. A considerable cause of that may have been that the p. p. chloroplasts are less hydrophilous than the spongy parenchyma chloroplasts. The number of the stroma thylakoids is lower than in the s. p. chloroplasts, which is in seeming contradiction to the high value of the chlorophyll a/b ratio. The full length of the partition per grana is considerably shorter than in the s. p. chloroplasts (cf.: Table 1).

Table 1. Analysis of the fine structure of choloplast

Species	Chloroplast	Chla/Chlb ratio	No. of thylakoids per granum	Partition lenght μ/granum	Partition length μ/u^2	Stroma lamellae μ/u^2	Partition per stroma lamellae
Hedera helix	spongy p.	3,6	34,5	0,56	16,1	4,0	4,03
	palisade p.	4,4	11,2	0,30	9,5	5,6	1,67
Nonea lutea	spongy p.	3,7	6,5	0,57	4,7	1,7	2,70
	palisade p.	4,5	5,6	0,39	7,6	3,2	2,39
Nuphar luteum	spongy p.	3,6	12,9	0,43	9,6	3,5	2,74
	palisade p.	6,0	3,5	0,46	5,4	1,9	2,81

3. Connection of the thylakoid aggregation with the chlorophyll a/b ratio

The fine-structure analysis of chloroplasts shows a highdegree, significant ($P > > 0.001$) difference in the spongy and palisade parenchymas. It is unambiguously proved by the above facts and the changes in pigment ratio that in the leaf a heterogeneous population is formed by the chloroplasts.

In the plants investigated, the chlorophyll a/b ratio of the spongy p. chloroplasts is smaller, and the full length of the partition per grana is larger in every case than in p. p. chloroplasts.

The percentage distribution of the number of thylakoids forming the grana shows similarly a great difference in the two tissues of mesophyll. The measure of the aggregation of thylakoids is also in a close correlation with the chlorophyll a/b ratio.

Table 2. Correlation of the total length of the partition per granum and the ratio of chlorophyll a/b

Species	Chloroplast	Partition number x length granum	Cholrophyll a/b
Hedera helix	spongy p.	18.76	3.6
	palisade p.	3.06	4.4
Nonea lutea	spongy p.	3.13	3.7
	palisade p.	1.79	4.5
Nuphar luteum	spongy p.	5.12	3.6
	palisade p.	1.15	6.0

Table 3. Percentage distribution of thylakoid aggregation and its correlation with the ratio of chlorophyll a/b

Species	Chloroplast	Measure of thylakoid aggregation in percentage			Chlorophyll a/b
		2—3 th.	4—6 th.	7<th	
Hedera helix	spongy p.	0	1.6	98.4	3.6
	palisade p.	4.2	8.2	87.6	4.4
Nonea lutea	spongy p.	7.0	17.2	75.8	3.7
	palisade p.	18.2	29.1	52.7	4.5
Nuphar luteum	spongy p.	0	10.8	89.2	3.6
	palisade p.	41.8	43.6	14.6	5.0

Our results agree with the establishments of Reger and Krauss (1969), Reyss and Bourdu (1970), Woo *et al.* (1970): The relative quantity of chlorophyll b increases parallel with the increasing aggregation of grana thylakoids.

It is known from the works of Boordman and Anderson (1964), Gross *et al.* (1966), Briantais (1968), Akoyunoglou and Argyroudi—Akoyunuglou (1974), as well as of others, that photosystem I is characterized by a high (Chlorophyll a/b= =6—7), and photosystem II by a low (Chlorophyll a/b=2—3) chlorophyll a/b ratio. If we compare the formation of pigment ratios and the analysis of the ultrastructure of the chloroplast with our knowledge obtained about the localization of the photosystems (8, 16, 24), we get the unequivocal answer that in the two tissues of mesophyll the ratio of the two photosystems is different. In the spongy p. chloroplasts the photochemical System II, in the palisade p. chloroplasts photosystem I predominates. According to Reeves and Hall (1973), photosystem II can probably produce as much ATP and NADPH as is sufficient for fixing CO_2.

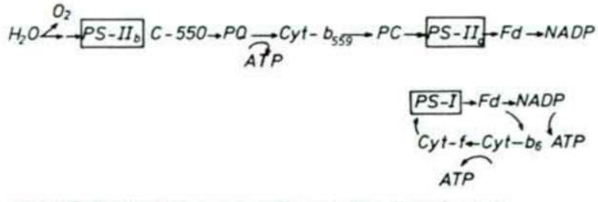

Fig. 2. Schema of photosystems according to Knaff and Arnon

4. Separation of photosystems and modification of their ratio

The question of photosystems I and II is an important problem which has not been chleared up as yet. It was demonstrated by KNAFF and ARNON (1969, 1971), ARNON (1971) that in photosynthesis there are three light-reactions (PS—II_b, PS—II_a and PS—I).

According to KNAFF and ARNON, the non-cyclic and cyclic photophosphorylations remain separate, and photosystem II is able to reduce NADP, even independently of PS—I.

The spatial separation of photosystems is supposed by GASANOV and FRENCH (1973). They established that the stroma lamella contained only photosystem I, but the grana thylakoids, however, contained both photochemical systems (PS—I and PS—II).

It appears from the above facts that the functional and structural separation of photosystems is very probable. The spatial separation is the first condition the modification of the photosystem ratios. In our opinion, the enrichment of photosystem I can take place in two ways:

a) By expanding the surface of the stroma lamellae;

b) By decreasing the degree of thylakoid aggregation when the ratio of the grana terminal membrane per partition is 2 to 1.

In the case of Hedera helix and Nonea lutea the length of stroma lamellae on the unit surface in the palisade p. chloroplasts is larger. The higher value of the ratio of photosystem I is therefore understandable.

The chlorophyll a/b ratio of the palisade p. chloroplasts in Nuphar luteum is prominently high: 6; the length of stroma lamellae falling to the unit surface is, on the other hand, shorter than in the spongy p. chloroplasts. The most likely possibility of solving the contradiction is that photosystem I is localized isolated in the grana terminal membranes as well.

The localization of the photochemical system I in the grana terminal membrane is shown by the thylakoid aggregation of all three plants, and it is prominently proved by the chloroplast of Nuphar luteum where 42 per cent of the thylakoids form grana consisting of two — three thylakoids.

An increase in the ratio of photosystem II can be carried out by increasing thylakoid aggregation or reducing and degrading the organization of stromal lamellae.

Making use of this opportunity, we wish to record our gratitude to research fellow FERENC JOÓ, junior research fellow IDA TÓTH, research student FLÓRA KÁLMÁN, secondary school mistress Katalin Szemenkei, laboratory technician MÁRTA FEJES for rendering possible and enabling the preparation of sections. Special thanks of the authors are due to junior lecturers IMRE ROJIK and IMRE HORVÁTH for the technical preparation of the electron-microscopic photographs.

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