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A remarkable constancy in the relative amount of stroma lamellae of chloroplasts from plants, and its functional significance.

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Introduction

The photosynthetic membrane system, the thylakoids, of plants consists of two main compartments, the grana (including the appressed grana core, the margins and the end membranes) and the stroma lamellae, which have specialised functions.

Methods

Quantitative evaluation was done on published electron micrographs in the following way. Parallel lines were drawn at regular intervals roughly perpendicular to the thylakoids and the number of intersections of each membrane type was counted. An intersection of an appressed membrane pair was counted as two intersections. The following types of membranes were distinguished: stroma lamella, appressed grana membranes together with grana margins, and grana end membranes. For each chloroplast between 600 and 1100 intersections were counted. References to publications with the electron micrographs used for the calculations are listed in the column to the right of Table I.

Results and Discussion

The relative amount of stroma lamellae is remarkably constant. For 28 chloroplasts from 16 different plants, the mean value of the percentage of stroma lamellae is 20.5 ± 2.0 (SD), See Table 1. This value is fairly independent of the size of the grana stacks (Fig.1) and must be of functional significance. It can be assumed that the length of a membrane seen in the electron microscope is proportional to its protein content of the membrane. Since the protein/chlorophyll ratio is higher for the stroma lamellae than the grana it can be estimated that only 16-18 per cent of the chlorophyll is located in the stroma lamellae. The remaining 82-84 per cent is in the grana. These values are supported by recent studies using confocal scanning laser microscopy (1) suggesting that *both* PS 1 and PS 2 are highly enriched in the grana

Table 1. Percentage of each membrane type of thylakoids from different plants (see methods).

Plant	Appressed + margins	End membrane	Grana total	Stroma lamellae	Reference
Spinach	70	8	78	22	3
Spinach	69	11	80	20	3
Spinach	63	19	82	18	3
Spinach	70	10	80	20	3
Spinach	63	17	80	20	3
Lettuce	70	11	81	19	3
Tobacco	60	22	82	18	3
Tobacco	69	12	81	19	Weibull unp.
Broad bean	63	17	81	19	9
Radish	66	11	77	23	10
Antirrum majus	73	4	77	23	3
Phleum pratense	69	11	80	20	3
Peperonia	69	10	79	21	3
Tanacetum	69	11	80	20	11
Tanacetum	62	15	77	23	11
Tanacetum	80	5	85	15	11
Sisymbrium	60	18	78	22	11
Sisymbrium	57	20	77	23	11
Brassica napus	65	14	79	21	12
Brassica napus	60	16	76	24	12
Brassica napus	69	10	79	21	12
Barley	73	7	80	20	3
Oat	69	11	80	20	3
Sugar cane*	69	8	77	23	3
Corn*	77	4	81	19	3
Arabidopsis	66	13	79	21	13
Arabidopsis	73	10	83	17	13
Arabidopsis	67	13	80	20	13

* mesophyll cells Mean value: 20.5 ±2.0

Fragmentation and separation analysis of thylakoids have shown that more chlorophyll is associated with PS 1 than with PS 2 (2-4). The excess is in the range 14-20 per cent, *i.e.* per 100 chlorophyll molecules 57-60 are associated with PS 1 and 40-43 with PS II. The same unequal distribution holds for carotenoids. Comparison between the absorption spectra of the different thylakoid vesicles led to the conclusion that the distribution of pigments between the two photosystems also gave a good estimate of the distribution of quanta absorbed by the two photosystems (4). In the case of spinach, PS 1 and PS II capture 59 and 41 per cent, respectively, of the total quanta received by the photosynthetic membrane in daylight (4).

Earlier observations using spectroscopic (5,6) and photoacoustic (7) measurements of quantum yield of the two photosystems can also be interpreted such that PS 1 receives more quanta than PS II.

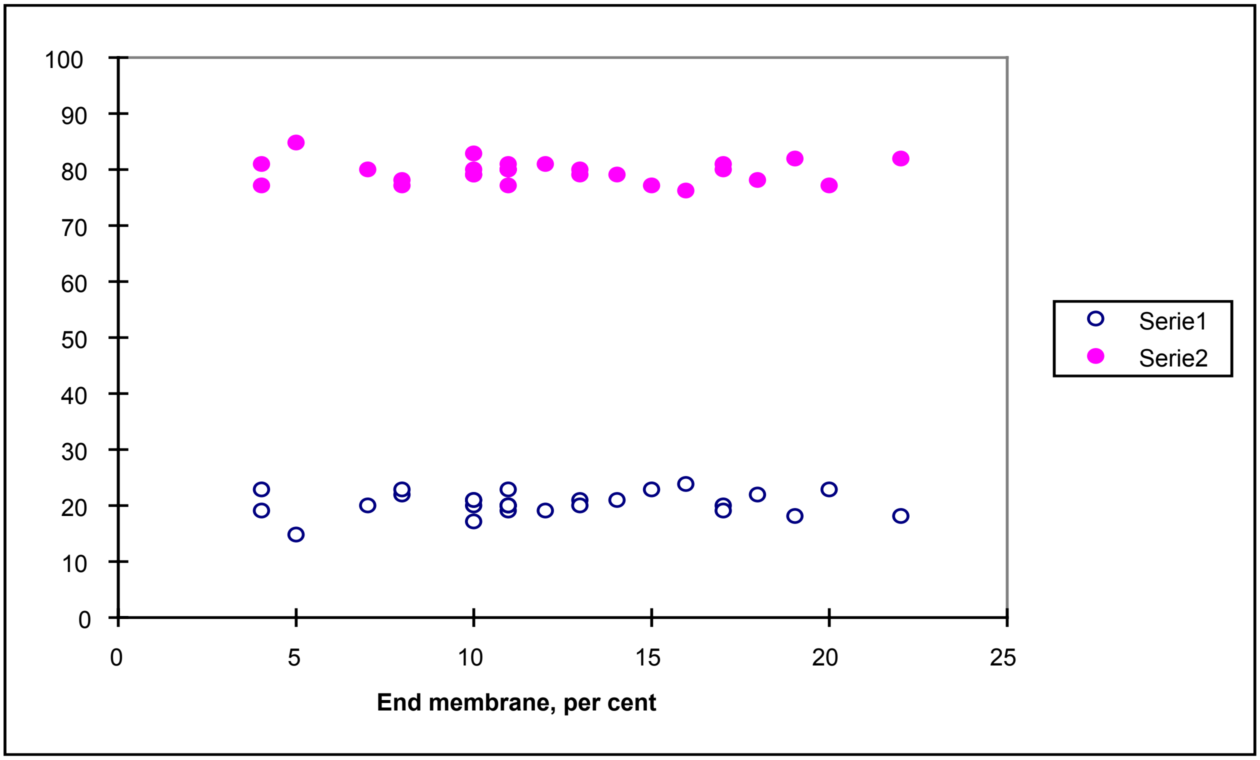

Fig.1. The size of the grana stacks vary between species and growth conditions. Chloroplasts from plants grown in low light have large grana with several discs (more than 20) layered upon each other while those from high-light plants may have only 2-4 . Despite this variation the percentage of grana (filled circles) and stroma lamellae (open circles) is remarkably constant. The percentage of end membranes, plotted on the x-axis, is a measure of the size of grana stacks; the more end membranes the smaller the grana stacks. Compare with table 1. Note the cluster of points around 10-12 per cent on the x-axis which corresponds to an average number of about 5-6 pairs of appressed membrane in the grana.

Based on these two observations - the constancy of the relative amount of stroma lamellae and the excess of chlorophyll associated with PS 1 - a quantitative model (8) for the thylakoid membrane has been proposed (see Fig. 2 in reference 8). According to this, 80 per cent of the membrane is in the form of grana and 20 per cent as stroma lamellae. Linear electron transport occurs in the grana where PS II, localised in the appressed core of the grana, co-operates with PS 1 in the margin which forms an annulus surrounding the grana core.
PS II of the appressed grana and PS 1 in the margin annulus are separated, yet most of them are in close contact. For geometrical reasons the contact area between the PS II and the PS 1 domains is relatively large which allows effective linear electron transport in microdomains involving both PS 1 and PS II (8). Only a minor fraction of PS II, i.e. those PS II units in the very centre of the grana disc, are without close contact with PS 1.

The stroma lamellae carry out cyclic electron transport coupled to ATP synthesis. This seems to be characteristic of single paired thylakoid membranes of higher plants (3,8).

A salient feature of the model is that it can explain why the quantum requirement for oxygen evolution is around 10 and that this value is almost constant for a large number of C3 plants. Assume that the linear electron transport in the grana has a requirement of 8 quanta per oxygen molecule . The additional quanta absorbed by PS 1 in the stroma lamellae - and used for cyclic electron transport only and not for oxygen evolution - will increase the quantum requirement to 9-10. Since the amount of stroma lamellae is fairly constant one should also predict the quantum requirement to be constant. This has indeed been found experimentally, the quantum requirement being between 9 and 10 for 37 species of C3 plants growing under widely different conditions (see ref.3 for references). An other important prediction of the model is that there is no need for long range electron transport between the appressed grana region and the stroma lamellae since the linear electron transport occurs within the grana. This is supported by recent studies on microdomains in thylakoids of higher plants (3,8)
More information on the model and references to earlier work can be found in a recent publication (8).

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